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PHYTOLOGIA

An international journal to expedite plant systematic, phytogeographical
and ecological publication

Vol. 80

April 1996

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NEW SPECIES AND COMBINATIONS IN *PSEUDOGYNOXYS* (SENECIONEAE)

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ABSTRACT

A new species of *Pseudogynoxys* s.l., *P. alajuelana* B.L. Turner, is described from Costa Rica. It belongs to a group of species that some workers would include in or near the recently described genera, *Garcibarrigoa* Cuatr. and *Talamancalia* H. Rob. & Cuatr., elements of which I position in an expanded *Pseudogynoxys*. To this end the following new combinations are proposed: *Pseudogynoxys westonii* (H. Rob. & Cuatr.) B.L. Turner, *comb. nov.*, and *P. durandii* (Klatt) B.L. Turner, *comb. nov.* So construed, *Pseudogynoxys* is conceived as a mesophytic genus of clambering shrubs and/or perennial herbs having mostly orange ray florets and variable style branches, the appendages of the latter varying from apically rounded and penicillate basally, to long-attenuate and sparsely penicillate along their margins.

KEY WORDS: Asteraceae, Senecioneae, *Pseudogynoxys*, *Garcibarrigoa*, *Talamancalia*, Costa Rica, systematics

Pseudogynoxys was first proposed by Greenman (1902) as a subgenus of *Senecio*. Cabrera (1950) elevated this to generic rank, the group largely recognized by its clambering or scandent habit, orange rays, and especially by its style branches which were thought to be rather uniformly bestowed with triangular styler appendages fringed at the base with a crown of hairs. Since Cabrera's treatment, several newly described genera (*Garcibarrigoa* Cuatr. and *Talamancalia* H. Rob. & Cuatr.) have been proposed that clearly relate to *Pseudogynoxys*, differing from the latter primarily in habit (non-clambering perennial herbs) and styler appendages. In my view (Turner 1991), *Garcibarrigoa* and *Talamancalia* are readily positioned in an expanded concept of *Pseudogynoxys*, unless one prescribes to a microgeneric concept for the numerous tropical American elements of *Senecio* as proposed by Nordenstam & Pruski (1995), Robinson & Cuatrecasas (1994) and perhaps others (Barkley, pers. comm.).

Much of the reasoning behind the generic splintering of the pseudogynoxoid alliance referred to above has to do with emphasis upon microcharacters, most notably

stylar branches and their appendages. Thus Pruski (1996), in his defense of the retention of *Garcibarrigoa*, notes that species of the latter "have neither the scandent habit nor the sterile triangular to acuminate style branch appendages tipped by a fringe or tuft of papillae, as typical of *Pseudogynoxys*." While his habitual observations are correct, my survey of style branches in the pseudogynoxoid alliance show a wide range of variation in this character, even within *Pseudogynoxys* (s.s.). For example, elongate stylar appendages with varying degrees of basal hairs, to those with merely rounded apices which are minutely papillate at base occur in *Pseudogynoxys* (s.s.). We (Mendenhall & Turner, in prep.) are currently undertaking a scanning electron microscopical study of the stylar appendages of the pseudogynoxoid complex and preliminary results suggest that stylar characters in this group are much more plastic than heretofore supposed, and that treatment of these taxa within an enlarged genus *Pseudogynoxys* will prove defensible on phyletic grounds.

PSEUDOGYNOXYS ALAJUELANA B.L. Turner, *spec. nov.* TYPE: COSTA RICA. Alajuela: P. Nac. Rincón de la Vieja. Quebrada Leiva. Colonia Blanca (10° 47' 20" N, 85° 15' 20" W), 600 m, 4 Apr 1991, *Gerardo Rivera 1235* (HOLOTYPE: MO!).

Similis *P. boquetensis* (Standl.) B.L. Turner sed habens capitula sine floribus radiantibus, appendices styli lineares-lanceolatas, et lobos corollarum faucibus ca. 1/3 plo longiores.

Perennial herbs 35-40 cm high. Stems densely hirsute with crinkly, purplish-septate, hairs. Leaves simple, gradually reduced upwards, those at mid-stem 8-10 cm long, 3-4 cm wide; petioles 2.0-2.5 cm long, auriculate at the base, subclasping but not connate; blades elliptic, pinnately veined, densely pubescent above and below, the margins irregularly serrate. Heads 2-4, arranged in loose corymbs, the ultimate peduncles mostly 3-10 cm long. Calyculus of 10-14 loosely arranged linear bracts 3-5 mm long. Involucre ca. 1 cm long, composed of ca. 11 lanceolate bracts. Ray florets absent. Disk florets 80-100 (est.); corollas tubular, glabrous, reportedly yellow, ca. 12 mm long, the throat poorly defined, 3-4 mm long, the lobes 5 ca. mm long, narrowly deltoid. Anthers ca. 2 mm long, basally obtuse or rounded, the apical appendages ca. 0.5 mm long. Style branches ca. 4 mm long, the appendages linear-lanceolate, hispidulous. Achenes (immature) 3-4 mm long, columnar, 8-10 costate, minutely appressed-pubescent; pappus of numerous delicate, white, readily deciduous bristles 10-12 mm long.

Pseudogynoxys alajuelana is an enigmatic species, possessing corolla and stylar characters which are seemingly attenuated forms of typical elements of the genus, but having the habit of those species that Robinson & Cuatrecasas (1994) recognize as the segregate genus *Talamancalia*. The corolla lobes of *P. alajuelana* are narrowly trianguloid and ca. 1/3 as long as the throat; the stylar branches have appendages that are linear-lanceolate and lack a well-defined basal tuft of hairs. Among most species of *Pseudogynoxys*, corolla lobes are narrowly triangular and usually 1/2 or more as long as the tube; the stylar appendages are usually narrowly deltoid to narrowly lanceolate, with often well-defined basal hairs. Nevertheless there is much variation in these two characters among the species I have examined, especially in the stylar appendages (as noted above) which may vary from merely trianguloid to lanceolate

with varying degrees of pubescence, occasionally within a single head. Regardless, I can not believe that the short corolla lobes and linear-lanceolate, weakly penicillate stylar branches of *P. alajuelana* are anything but accentuations of trends already present in *Pseudogynoxys* s.s.. The habit of *P. alajuelana*, a perennial non-clambering herb ca. 40 cm high, to judge from the single specimen examined, is that found in the recently proposed *Talamancalia* (Robinson & Cuatrecasas 1994). Additionally, *Pseudogynoxys alajuelana* has leaves similar to *Talamancalia boquetensis* (Standl.) H. Rob. [= *Pseudogynoxys boquetensis* (Standl.) B.L. Turner], possessing subclasping basal appendages, (as do some species of *Pseudogynoxys*, as noted by Robinson & Cuatrecasas 1994).

Various authors might possibly consider the present novelty to be yet another closely related monotypic genus, if emphasis is placed upon the stylar appendages and corolla lobes possessed by *Pseudogynoxys alajuelana*, for Robinson & Cuatrecasas (1995) note that

The five genera, *Garcibarrigoa*, *Jacmaia*, *Jessea*, *Pseudogynoxys*, and *Talamancalia*, differ from almost all species of *Senecio* sensu stricto by having long and narrow lobes on the corolla. The lobes in *Jacmaia* and all of *Jessea* except the type species are about as long as the throat. The limbs and the lobes of the corolla of *Garcibarrigoa* are comparatively short with the lobes narrowly triangular rather than narrowly oblong.

My own view is that the habit and short corolla lobes of *Pseudogynoxys alajuelana* vitiate recognition of a monotypic *Garcibarrigoa*. Indeed, I believe that phyletic studies emphasizing similarities (instead of differences) among the several taxa mentioned in the above will show that *Pseudogynoxys*, *Garcibarrigoa*, and *Talamancalia* are more closely related among themselves than they are to *Jacmaia* and *Jessea*. DNA studies are sorely needed to help ferret out relationships among these various generic segregates.

In line with the above taxonomic views I propose the following new combinations:

PSEUDOGYNOXYS WESTONII (H. Rob. & Cuatr.) B.L. Turner, *comb. nov.*
BASIONYM: *Talamancalia westonii* H. Rob. & Cuatr., Novon 4:52. 1994.

PSEUDOGYNOXYS DURANDII (Klatt) B.L. Turner, *comb. nov.*
BASIONYM: *Senecio durandii* Klatt, Bull. Soc. Bot. Belg. 31:211. 1892.

This Costa Rican endemic is a suffruticose herb with pendant branches having orange ray and disk florets and emits "an unpleasant odor when crushed" (*Almeda* 5791 [TEX]; described as that of "culantro" by *Grayum* 3746 [TEX]). Standley (1938) notes the species to be "a most distinct one, altogether unlike any other with which I am familiar." He also adds that the plant appears to be rare occurring "on rocks at the edge of streams in deep, dark forests, sometimes in the spray of waterfalls." This is also borne out by label data on the ten or more sheets known to me (LL, MO, TEX).

Of the species to be included within my treatment of *Pseudogynoxys* for Costa Rica (in prep.) this is the most distinctive, but it appears to me to fall within the pseudogynoxoid alliance as conceived here.

ACKNOWLEDGMENTS

I am grateful to Gayle Turner for the Latin diagnosis, and to Ted Delevoryas for reviewing the manuscript. Maria Thompson provided the illustration.

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REVISION OF *DESMANTHODIUM* (ASTERACEAE)

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ABSTRACT

The genus *Desmanthodium* (Asteraceae, Heliantheae) is treated as having seven species, six of these indigenous to México and Central America, and one to South America. The recently described *D. congestum* Arriagada & Stuessy, is believed to be the same as *D. tomentosum*. A key to the species, selected illustrations, and complete synonymy are provided, along with dot maps showing their distribution.

KEY WORDS: Asteraceae, Heliantheae, *Desmanthodium*, México, systematics

The present study has been occasioned by my treatment of the tribe Heliantheae for the Asteraceae of Mexico (*cf.*, Turner 1996). As conceived here, *Desmanthodium* is a small mostly montane genus of seven species, six of these native to México. The species are very closely related, and if partitioned into infrageneric components they would seem to fall into two groups: a strictly herbaceous element, *D. ovatum* Benth., with the remainder forming a subclade of robust suffrutescent herbs, subshrubs or shrubs to 4 m high.

Desmanthodium was first proposed by Bentham in 1876 with the description of two Mexican species, *D. perfoliatum* Benth. and *D. ovatum*, the former subsequently selected as the generitype. These were positioned by Bentham (*Genera Plantarum*, 1876) in the tribe Heliantheae, subtribe Milleriinae, between the genera *Riencourtia* and *Clibadium*. Thereafter, among the species recognized here, Hemsley added *D. guatemalense* Hemsl. in 1881; Greenman proposed *D. fruticosum* Greenm. in 1903; T.S. Brandegee described *D. tomentosum* T.S. Brandegee in 1914; Blake in 1924 conjured up *D. blepharodon* S.F. Blake, and Turner concocted *D. hintoniorum* B.L. Turner in 1996. A few other names have been proposed, but these have been treated as synonyms.

There has been no revision of the genus prior to the present study, although Robinson (1981) provided a succinct account of its subtribal position, as noted under comments presented below (*cf.*, Generic Relationships).

CHROMOSOMES

As indicated in the list of chromosome counts tabulated below, all counts were determined from meiotic material. Fay (1974) was the first worker to report a chromosome number for *Desmanthodium*, this being a count of $n=18$ pairs for *D. fruticosum*. Subsequent workers have confirmed this number for the genus, except for Ralston, *et al.* (1989) who report a count of $n=17$ pairs for *D. fruticosum*. The latter count should be confirmed since it does not agree with previous reports and was not documented by photographs or camera lucida drawings. In fact, none of the counts in *Desmanthodium* has been documented by photographs or illustrations.

CHROMOSOME COUNTS FOR *DESMANTHODIUM*

<i>D. fruticosum</i> $2n=36$	Fay (1974)	Oaxaca: Cronquist 10855
<i>D. fruticosum</i> $2n=36$	Keil & Stuessy (1977)	Mexico: Stuessy 3129
<i>D. fruticosum</i> $2n=36$	Keil, <i>et al.</i> (1988)	Guerrero: Keil 15356
<i>D. fruticosum</i> $2n=34$	Ralston, <i>et al.</i> (1989)	Guerrero: Turner 15876
<i>D. perfoliatum</i> $2n=36$	Sundberg, <i>et al.</i> (1986)	Oaxaca: Turner 80A
(reported as <i>D. caudatum</i>)		

GENERIC RELATIONSHIPS

Robinson (1981) recognized *Desmanthodium*, along with *Stachycephalum*, as the only two genera in his subtribe Desmanthodiinae, numbered 6 from among 32 subtribes in his breakdown of the tribe Heliantheae. *Desmanthodium* differs markedly from *Stachycephalum* in having its ray florets completely enclosed in a sac or vesicle, in addition to yet other characters discussed by Robinson. He reckoned the Desmanthodiinae to be closely related to his subtribe number 7, the Clibadiinae, which contained three genera (*Clibadium*, *Lantanopsis*, and *Riencourtia*).

Nearly all workers would agree that the two subtribes recognized by Robinson are highly specialized. Indeed, Robinson (1981, p. 40) conjectures that the so called vesicle which houses the ray florets in *Desmanthodium* might actually be a loosened part of the ovary wall, as opposed to an enveloping involucre bract or phyllary; so interpreted this would be a unique feature in the Asteraceae. Whether or not *Stachycephalum* is properly positioned with *Desmanthodium* in the subtribe Desmanthodiinae is moot; it might with equal morphological justification be included with or near *Clibadium* or *Lantanopsis* in the subtribe Clibadiinae. The probable base chromosome number of *Desmanthodium* ($x=18$) differs from that of *Clibadium* ($x=16$, cf. Stuessy & Arriagada 1993) and *Riencourtia* ($x=ca. 16$); unfortunately chromosome counts for *Stachycephalum* are unreported.

TAXONOMY

DESMANTHODIUM Benth.

Suffruticose stiffly erect perennial herbs to 1 m high, or erect to sprawling shrubs or subshrubs to 4 m high. Leaves simple, opposite throughout, subpinnately nervate with usually 3 prominent nerves from above the base. Heads ill-defined, arranged in congested bracteate glomerules, the glomerules in turn disposed in very open cymose panicles, or relatively congested in flat-topped cymes. Involucral bracts 1-3, separate to the base, not forming a clearly defined involucre. Receptacle plane, epaleate, except for an outer series of pales which completely enwrap the subtended ray florets. Ray florets 1-3, pistillate, fertile, enclosed in sac-like bracts; corollas ca. 1 mm long, the ligule absent or nearly so. Disk florets 5-10 per head, perfect but sterile, the ovaries elongating with age; corollas small, white, 5-lobed; tubes about as long as or somewhat longer than the funnelform or campanulate throats. Achenes lenticular, black, minutely striate, completely enclosed in a persistent papery sac. Base chromosome number, $x=18$.

Type species, *Desmanthodium perfoliatum* Benth.

KEY TO SPECIES

1. Suffruticose herbs with slender simple stems 0.4-1.0 m high. 1. *D. ovatum*
1. Shrubs, or arching to sprawling thick-stemmed shrublets 1-4 m high. (2)
 2. Leaves sessile, those at midstem clearly perfoliate. 2. *D. perfoliatum*
 2. Leaves petiolate, never perfoliate. (3)
3. Stems and branches of the capitulescence glabrous; heads on thick stout peduncles, scarcely exceeding the foliage; Oaxaca, México (Mpio. Miahuatlán). 3. *D. hintoniorum*
3. Stems and branches of the capitulescence clearly pubescent, either in lines or throughout. (4)
 4. Uppermost stems and branches of the capitulescence tomentose throughout, the vestiture mostly 0.5-0.7 mm high; southwesternmost Chiapas, México and closely adjacent Guatemala. 5. *D. tomentosum*
 4. Uppermost stems and branches of the capitulescence pubescent in lines, the vestiture mostly 0.2-0.4 mm high; widespread. (5)
5. Leaves on primary stems mostly thin, the blades 5-10(-15) cm long, decidedly ovate, widest near base or well below the middle (rarely not); Pacific montane slopes of western México from Durango to Oaxaca. 4. *D. fruticosum*
5. Leaves on primary stems mostly thick (subsucculent), the blades (10-)15-20 cm long, elliptical, mostly widest at or near the middle; Guatemala, Honduras, El Salvador and South America. (6)
 6. Leaves on primary stems with blades gradually tapering, ciliate at the base, the petioles 3-15 mm long; Venezuela. 7. *D. blepharodon*

6. Leaves on primary stems with blades not tapering upon the petioles, glabrous at the base, the petioles 1-5 mm long; Guatemala, Honduras and El Salvador. 6. *D. guatemalense*

1. *DESMANTHODIUM OVATUM* Benth., Hook. Icon. Pl., t. 1116, 1872. Fig. 1. TYPE: MEXICO. Oaxaca: "woods of the province of Oaxaca", 7000-8000 ft, Nov-Apr 1840, *Galeotti* 2081 (LECTOTYPE [selected here]: K; Photoislectotype: MICH!). Two collections were cited in the protologue, that selected here as lectotype and *Andrieux* 319 from the Sierra San Felipe, Oaxaca. *Desmanthodium lanceolatum* Greenm., Proc. Amer. Acad. Arts 34:576. 1899. TYPE: MEXICO. Morelos: mountains above Cuernavaca, 2100 m, 9 Aug 1898, *C.G. Pringle* 6940 (HOLOTYPE: MO; Isotype: UC!).

Perennial glabrous herbs with simple, mostly unbranched stems 20-100 cm high; roots thickened, fasciculate or arising from short stout rhizomes (cf., *Ilitis* 1289 [TEX]). Stems sparsely puberulent to glabrate, 2-4 mm thick below. Leaves well-spaced along the stem, mostly shorter than the internodes, those at midstem mostly 5-15 cm long, 3-6 cm wide; petioles 5-35 mm long; blades ovate to subdeltoid, gradually or abruptly tapering upon the petioles, glabrous or nearly so. Heads arranged in relatively few, long-pedunculate aggregations. Outer and interior bracts of the aggregations ovate, subsucculent, their apices white or whitish. Heads 8-24 in any one aggregation, the whole superficially resembling a head (syncephalum), these borne upon peduncles 1-8 cm long. Heads with 1-3 pistillate florets and 12-16 sterile disk florets. Achenes flattened tangentially, ca. 3 mm long, 1.5 mm wide, encased in sac-like sparsely pubescent involucre bracts.

DISTRIBUTION (Figure 5) AND ECOLOGY: México State, Morelos, Puebla and Oaxaca, mostly oak woodlands, 2000-2600 m, Jul-Aug.

REPRESENTATIVE SPECIMENS: MEXICO. México State: *Rzedowski* 30918 (LL,MEXU). Puebla: *Tenorio* 7492f (TEX). Oaxaca: *Panero* 3617 (TEX); *Pringle* 4694 (LL,MEXU); *Soule* 2422 (MEXU,TEX).

This species is well represented in herbaria and, because of its herbaceous habit, relatively easily recognized. Most collectors note the plants to be between 20-100 cm high; however, label data on *Hinton* 2758 (LL) records the plant to be 1.5 m high, but this is not evident from the sheet concerned.

I am unable to distinguish *Desmanthodium lanceolatum* from *D. ovatum*. The former name has been applied to plants having leaf forms with lanceolate to narrowly ovate blades which taper upon the petioles. Both leaf forms may occur in the same general region and intergrades between such forms occur. Exceptionally petiolate blades of *D. ovatum* also occur (Figure 1), but most collections lie somewhere between these extremes, the blades at midstem usually gradually tapering upon the petioles.

One might consider erecting a monotypic section to house *Desmanthodium ovatum*, for it is sufficiently distinct from the shrubby elements of *Desmanthodium* to perhaps warrant such recognition. Its habit, relatively few aggregations to a capitulescence and generally more numerous staminate florets are diagnostic.

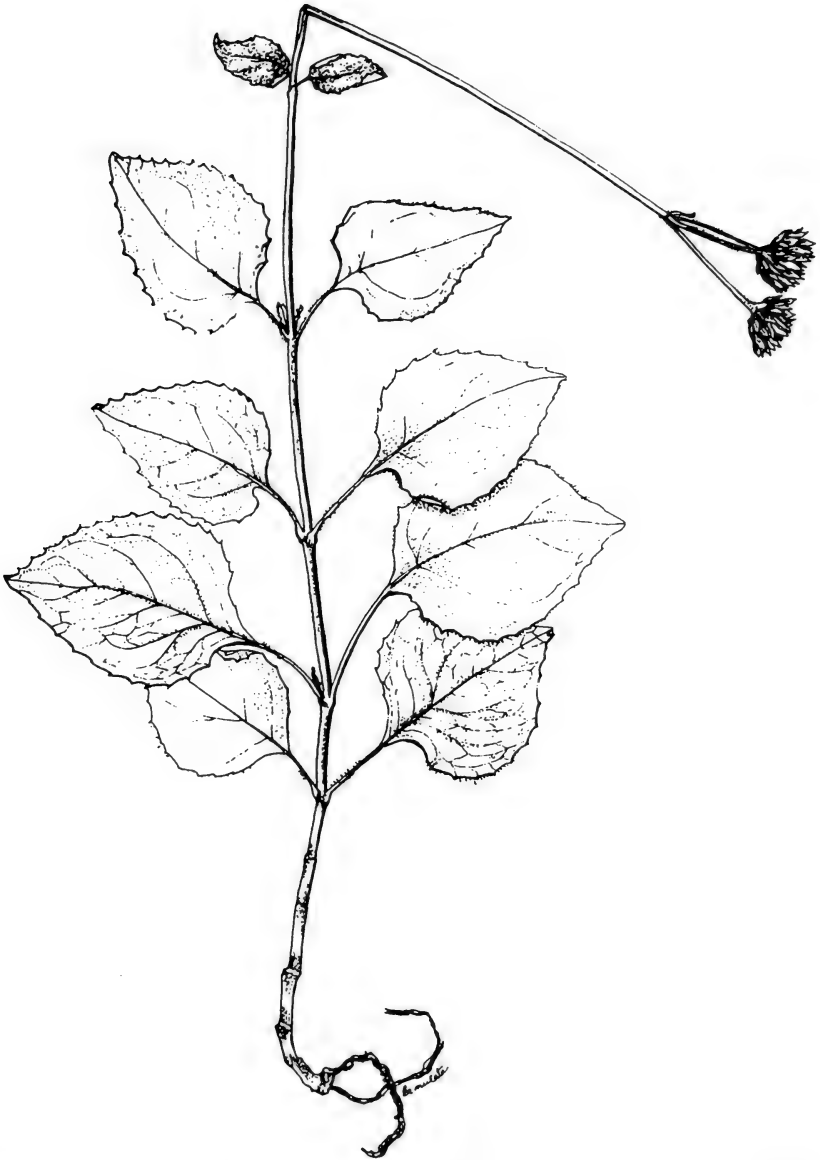


Figure 1. *Desmanthodium ovatum* (Panero 3617).

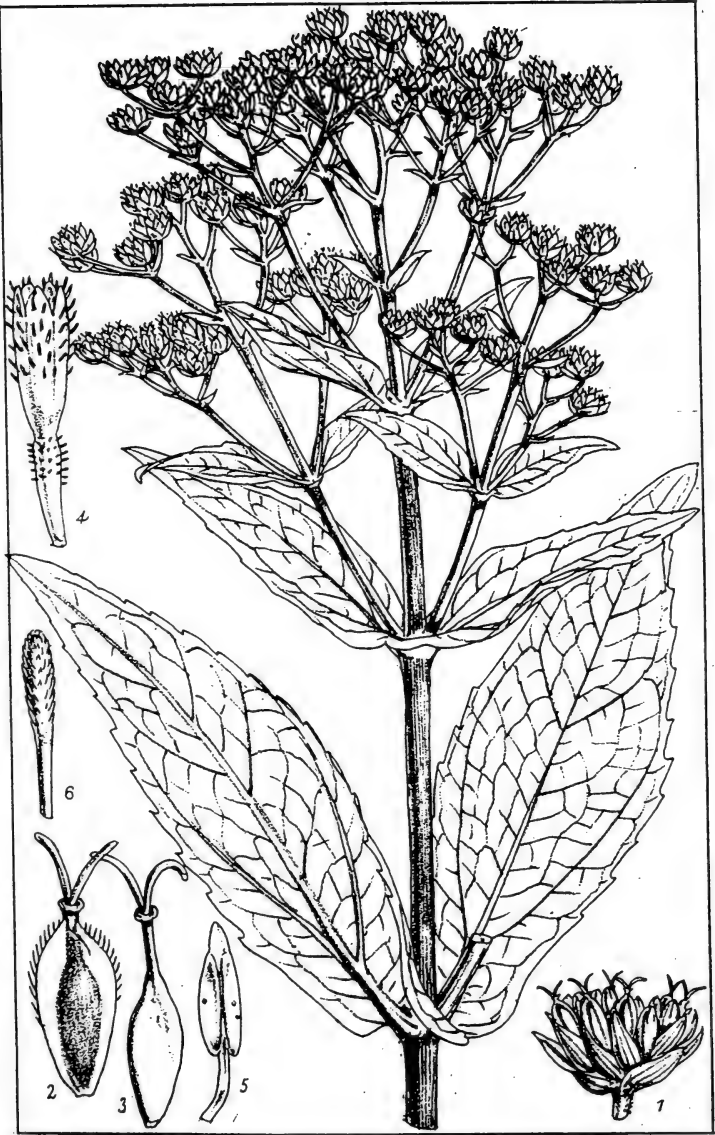


Figure 2. *Desmanthodium perfoliatum* (t. 1116, 1887).

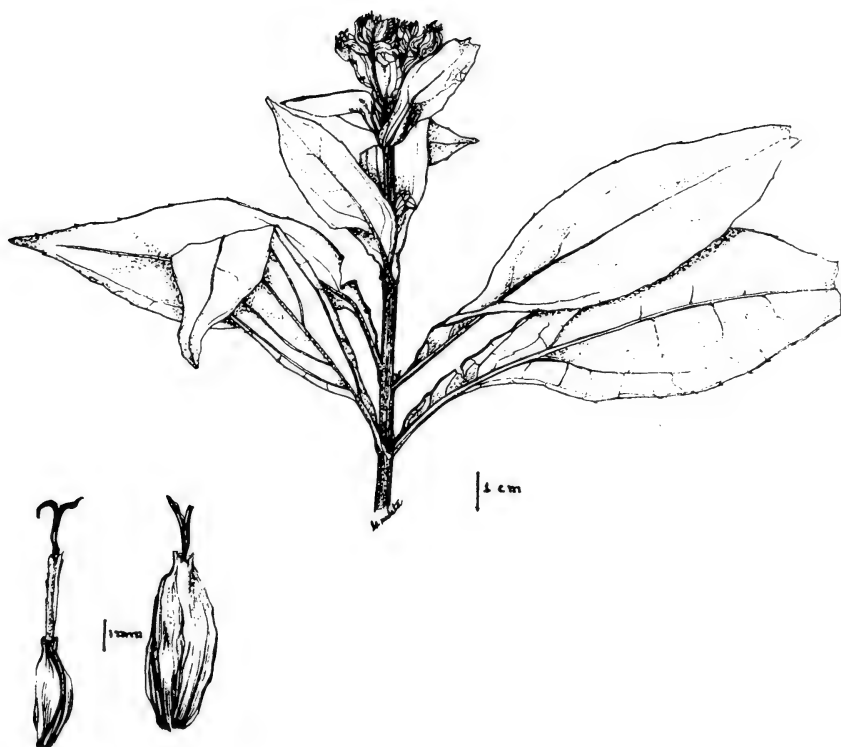


Figure 3. *Desmanthodium hintoniorum* (holotype).



Figure 4. Distribution of *Desmanthodium fruticosum* (open circles); *D. guatemalense* (open triangles); *D. hintoniorum* (closed triangle); *D. tomentosum* (closed circles).

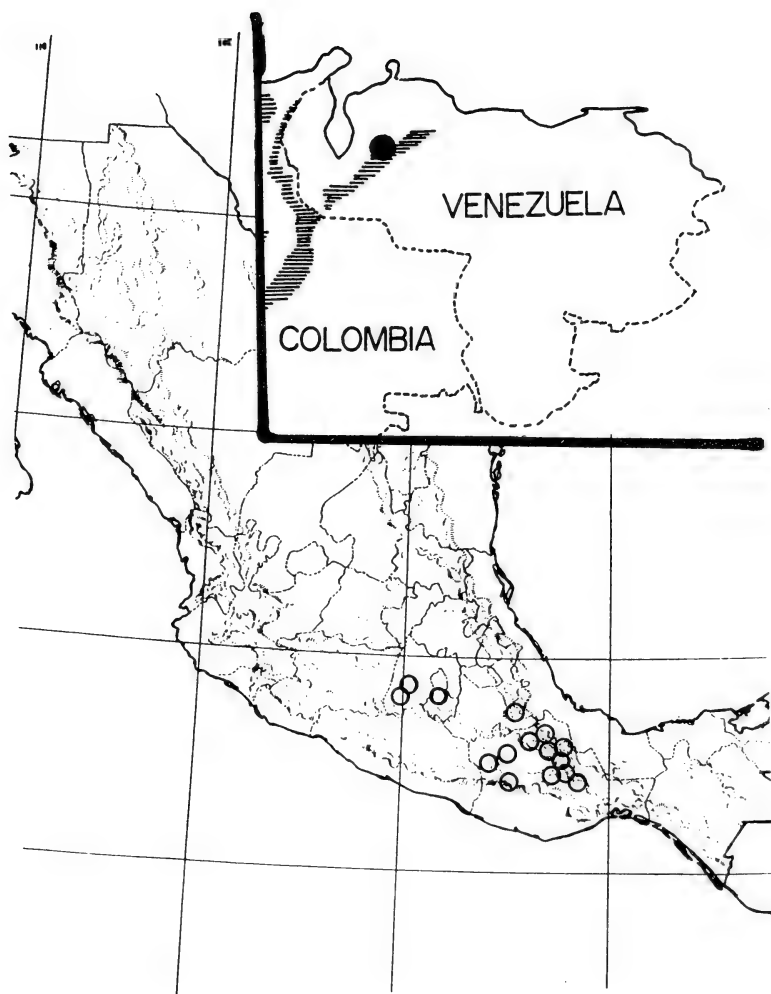


Figure 5. Distribution of *Desmanthodium ovatum*; inset, *D. blepharodon* (South America).

2. *DESMANTHODIUM PERFOLIATUM* Benth., Hook. Icon. Pl. 12:15. t. 1116. 1887. TYPE: MEXICO. Oaxaca: w/o specific locality, 4500 ft, 1835-1840, H.G. Galeotti 2050 (HOLOTYPE: K).
Flaveria perfoliata Klatt, Leopoldina 23:146. 1887. TYPE: MEXICO. Oaxaca(?): "Cumbre de Estepe", 1841-43, F.M. Liebmann 482 (LECTOTYPE [selected here]: GH!). Rydberg (1915) was the first to call attention to the synonymy listed here.
Desmanthodium caudatum S.F. Blake, J. Wash. Acad. Sci. 28: 488. 1938. TYPE: MEXICO. Chiapas: Escuintla, Finca Juárez, 12 Aug 1937, E. Matuda 1750 (HOLOTYPE: US!; Isotype: MEXU; Fragment holotype: LL!).

Shrublets or shrubs 1-4 m high. Much resembling *Desmanthodium guatemalense* but the leaves relatively thin and clearly perfoliate, the blades united below, not at all petiolate, and heads more numerous; chromosome number, $2n = 36$.

DISTRIBUTION (Figure 6) AND ECOLOGY: Guerrero, Oaxaca and Chiapas in pine-oak forests, 900-1700 m; Jul-Nov.

REPRESENTATIVE SPECIMENS: MEXICO. Guerrero: 15.8 mi by road from Chilpancingo west towards Omiltemi, pine-oak forest, 2000 m, rare among limestone boulders, 27-28 Jul 1968, Anderson 4935 (MICH). Oaxaca: Sierra San Felipe, 7500 ft, 13 Aug 1894, Pringle 4799 (MICH); 3.6 mi SW of Suchixtepec along road to Puerto Angel, 22 Aug 1980, Turner 80A-11 (TEX). Chiapas: Mpio. Bochil, 4 mi NE Bochil, 4500 ft, 21 Aug 1965, Breedlove 12073 (LL, MICH); ca. 16 mi W of San Cristóbal de las Casas, 26 Aug 1976, Hartman 4179 (TEX); Mpio. Amatenango del Valle, 5900 ft, 5 Sep 1966, Ton 1104 (LL).

Like *Desmanthodium fruticosum*, *D. perfoliatum* is a highly variable, relatively common species, especially in Chiapas. Only a single collection is known from Guerrero (cited above) where it was reported to be "Rare, seen once." The plant concerned has relatively narrow thin leaves (on secondary shoots), the blades markedly narrowed below with weakly developed auriculate-perfoliate bases. Specimens identified as *D. caudatum* are robust with very large, relatively thin leaves, but similar leaf forms occur across the range of the species (e.g., in Oaxaca, Turner 80A-11, cited above), and there seems little justification for its recognition.

3. *DESMANTHODIUM HINTONIORUM* B.L. Turner, Phytologia 79:317. 1996. Figure 3. TYPE: MEXICO. Oaxaca: Mpio. Miahuatlán, La Sirena, 2525 m, 23 Oct 1995, Hinton, et al. 26409 (HOLOTYPE: TEX!).

Shrub to 1.5 m high, the stems clearly woody and glabrous throughout. Leaves mostly 10-12 cm long, 3.0-3.5 cm wide; petioles 2-4 mm long; blades narrowly elliptical, pinnately nervate, gradually tapering upon the petioles, the margins with minute well-spaced, denticulate teeth, but seemingly entire upon superficial inspection. Heads much-congested and terminal on stout peduncles 0.5-2.0 cm long, the syncephalous structure ca. 1.5 cm high and 2-3 cm across. Bracts ovate, glabrous, subcoriaceous, 8-10 mm long, 5-6 mm wide, not forming a well-defined involucre bound head. Receptacle plane, glabrous. Pistillate florets 2, fertile; ligule absent, the tube ca. 1.5 mm long; achenes ellipsoid, glabrous, completely enclosed in fused, elliptical (in outline) bracts, the latter 6-7 mm long, ca. 2.5 mm wide, glabrous

throughout. Disk florets ca. 8, sterile, the style branches fused, forming a conical brush ca. 2 mm long; corollas white, glabrous, 5-lobed, the lobes ca. 1.4 mm long with ill-defined veins, these scarcely marginal, if at all; base of style surrounded by a well defined nectary ca. 0.75 mm high. Achenes of disk florets elongating at anthesis up to several times their bud-size so as to resemble stout stalks 5-10 mm long.

DISTRIBUTION (Figure 4) AND ECOLOGY: known only from type material.

As noted in the original description, this taxon is closely related to the more southern, *Desmanthodium guatemalense*; it differs in having narrower, more elliptical, nearly entire leaves, and being glabrous throughout, including all floral parts.

4. *DESMANTHODIUM FRUTICOSUM* Greenm., Proc. Amer. Acad. Arts 40:37. 1904. TYPE: MEXICO. Jalisco: Zapotlán, 9 Oct 1903, *E.W.D. Holway 5137* (HOLOTYPE: GH!).

Sprawling or arching shrubs or subshrubs 0.5-4.0 m high. Young stems pubescent in lines with crinkly brownish or tannish hairs, the vestiture mostly 0.3 mm high or less. Midstem leaves (of primary shoots) mostly 8-17 cm long, 3-7 cm wide; petioles 3-10 mm long; blades ovate to ovate-elliptic, sparsely appressed-pubescent beneath along the major veins, the margins variously dentate. Heads aggregated, the aggregations arranged in terminal rounded corymbose panicles 15-30 cm high and about as wide. Involucres subtended by 1-3 leathery, whitish, broadly ovate bracts, at anthesis mostly 4-6 mm long, 2-4 mm wide. Ray florets 1, pistillate fertile. Disk florets 4-8, the corollas white, 2-4 mm long, sparsely pubescent to nearly glabrous; lobes ca. 0.8 mm long. Chromosome number, $2n=36$.

DISTRIBUTION (Figure 4) AND ECOLOGY: Western México from Durango to Oaxaca, occurring in pine-oak woodlands, 1800-2400 m; Aug-Oct.

REPRESENTATIVE SPECIMENS: MEXICO. Durango: "near summit on Durango Road," 10 Oct 1955, *Templeton 7643* (MICH). Nayarit: ca. 10 road mi E of Jacocotlán, on road to Tepic, 4 Oct 1952, *McVaugh 13360* (MICH). Jalisco: ca. 10 mi SSE of Autlán, 29 Sep 1960, *McVaugh 19548* (LL,MICH). Colima: 22 km NNW of Colima, Rancho El Jabali, 26 Aug 1988, *Sanders 8366* (TEX). Michoacán: Mpio. Coalcomán, 15.1 mi SW of Coalcomán, 12 Sep 1985, *Luckow 2915* (TEX). México: 12.5 mi SW of Temascaltepec, 12 Oct 1966, *Anderson 3945* (MICH). Guerrero: 62 road mi N of Acapulco, 20 Oct 1962, *Cronquist 9706* (MICH,NY,TEX). Oaxaca: ca. 10 mi N of Putla, 30 Oct 1970, *Cronquist 10855* (MICH,NY).

This species is represented in herbaria by numerous collections and is nicely illustrated by McVaugh (1984). The foliage is quite variable, leaves on secondary shoots being smaller and narrower than those on primary shoots. It is superficially similar to the shrubby *Desmanthodium perfoliatum*, the latter readily distinguished by its markedly perfoliate leaves. Occasional plants of *D. fruticosum* may possess ternate leaves (e.g., *Sundberg 2988* [NY]).



Figure 6. Distribution of *Desmanthodium perfoliatum*.

Desmanthodium fruticosum is closely related to *D. guatemalense* and the two might be reasonably combined. Both have shrubby habits and similar foliage, but the leaves of the latter are generally larger, thicker, and more nearly elliptic and less tapered at the base. Leaves on secondary shoots of both species tend to be smaller and narrower, making distinctions between these difficult. The two taxa are seemingly best distinguished by characters of the capitulescence, those of *D. fruticosum* possessing generally more numerous, smaller ultimate glomerules, the latter arranged in larger, more open, rounded cymose panicles. But, it must be admitted that occasional plants of *D. fruticosum* (e.g., *Templeton 7643* [MICH], from Durango), were these collected in Guatemala, because of their large heads and foliage, would surely have been annotated as *D. guatemalense*.

5. *DESMANTHODIUM TOMENTOSUM* T.S. Brandege, Univ. Calif. Publ. Bot. 6:73. 1914. TYPE: MEXICO. Chiapas: Cerro del Boquerón, Sep 1913, *Purpus 6683* (HOLOTYPE: UC!).

Desmanthodium congestum Arriagada & Stuessy, Brittonia 42:283. 1990. TYPE: MEXICO. Chiapas: San Vicente, 500 m, Aug 1938, *E. Matuda 2508* (HOLOTYPE: GH; Isotypes: LL!, MICH!).

Shrubs or subshrubs 1-3 m high; much resembling *Desmanthodium guatemalense* but the leaves thinner with somewhat larger blades which gradually taper onto the petioles, the latter 15-50 mm long; in addition the branches of the capitulescence are pubescent throughout (as opposed to pubescent in lines) with spreading tomentose hairs, as are the major veins beneath the blade.

DISTRIBUTION (Figure 4) AND ECOLOGY: Known only from southwesternmost Chiapas and closely adjacent Guatemala in pine-oak forests, 1500-2200 m; Aug-Nov.

REPRESENTATIVE SPECIMENS: MEXICO. Chiapas: Mpio. de Unión, Faldas del Volcán Tacana, 1500-1680 m, 18 Oct 1985, *Villaseñor Rios 864* (MEXU, TEX); SE side of Volcán Tacana above Talquian, 2200 m, 12 Nov 1972, *Breedlove 29482* (MO).

GUATEMALA: Prov. San Marcos: Finca Armenia, San Rafael pie de la Cuesta 10 Carrizal, past finca Africa, 1300-1600 m, 9-12 Aug 1980, *Dwyer 15316* (MO).

Arriagada & Stuessy (1990) thought their newly described *Desmanthodium congestum* to be sufficiently distinct so as to belong to a newly erected section *Multiaggregata*. They compared their taxon with both *D. tomentosum* and *D. perfoliatum*, noting its closer relationship with the former. Indeed, I am unable to distinguish *D. congestum* from *D. tomentosum*; their emphasis upon the more congested heads of the former is, in my opinion, illusionary, there being much variability and interpretational errors involved in ascertaining the number of heads involved in the ultimate aggregations of any given capitulescence, these varying from 4 to 24.

Desmanthodium tomentosum is sufficiently close to *D. guatemalense* so that a case might be made for their treatment as but varieties of a single species. Indeed, the type

of *D. congestum* itself, in pubescence, stands somewhere between these two taxa, although somewhat closer to *D. tomentosum* in leaf shape and texture.

6. *DESMANTHODIUM GUATEMALENSE* Hemsl., Biol. Centr. Amer. Bot. 2:142. t. 45. 1881. TYPE: GUATEMALA. Sacatepéquez: Volcán de Fuego, 6000 ft, (1860-1865), *Salvin s.n.* (HOLOTYPE: K).
Desmanthodium hondurensis A. Molina, Ceiba 11:70. 1965. TYPE: HONDURAS. Comayagua: Barranco Trincheras, 1200 m, 28 Dec 1952, *Williams & Williams 18701* (HOLOTYPE: F).

Stiffly erect to subscandent shrubs to 3 m high. Much resembling *Desmanthodium fruticosum* but the midstem leaves mostly thicker, more nearly elliptic, broadest at or near the middle, the petioles shorter (unwinged portion), and the heads generally larger, arranged in rather flat-topped or broadly rounded capitulescences, mostly broader than wide.

DISTRIBUTION (Figure 4) AND ECOLOGY: Thickets along streams and slopes of volcanic cones, reportedly growing on volcanic ash in montane forests, 1200-3000 m; Jul-Nov.

REPRESENTATIVE SPECIMENS: GUATEMALA. Baja Verapaz: *King 3293* (TEX,UC). Chiquimula: *Molina R. 26812* (US). San Marcos: *Dwyer 15316* (US). Sacatepéquez: *Croat 41985* (MO,US). Suchitepéquez: *Skutch 1515* (LL).

HONDURAS: Comayagua: *Molina R. 31656* (MO). Itibuca: *Rodríguez 81* (MO). Ocotepeque: *Molina R. 30886* (MO).

EL SALVADOR: Santa Ana: *Croat 42367* (UC).

Typical elements of this Central American species (as shown in Figure 4), possess large relatively thick leaves upon their primary stems, the blade tapering upon the petiole nearly to its base. Additionally, the heads are arranged on relatively short, thick branches which tend to form a stout, broad, somewhat flattened capitulescence. Nevertheless, secondary branches often possess much smaller leaves, the blades gradually tapering upon longer petioles. The latter, often populational, forms have been given the name *Desmanthodium hondurensis*. Such forms are vegetatively very similar to *D. fruticosum*, but the two taxa are readily distinguished by their capitulescence, as noted in the above. Leaf variation on primary and secondary branches of *D. guatemalense* is neatly illustrated by M. Pahl in his delineation of the species for the Flora of Guatemala.

7. *DESMANTHODIUM BLEPHARODON* S.F. Blake, J. Wash. Acad. Sci. 14:454. 1924. TYPE: VENEZUELA. Trujillo: "Between La Puerta and Timotes", 2000 m, 16 Sep 1922, *Alfredo Jan 1143* (HOLOTYPE: US).

Much resembling *Desmanthodium guatemalense* but the leaves reportedly thicker, ovate, with 3-5 principal nerves, the blades broader near the base and pubescent along the lower margins; additionally the heads appear to be arranged in a rather evenly-

fasciculate manner, resembling the capitulescence of species belonging to the remotely related genus *Stevia*.

DISTRIBUTION (Figure 5) AND ECOLOGY: Known from only a few collections in Venezuela where it is "endémica de los páramos", according to Aristeguieta (1964); Sep.

According to its author, this taxon is nearest *Desmanthodium guatemalense*, the latter having "glaucous branches and thin-membranous, more or less rhombic-ovate, sessile leaves which are not ciliate at the base." *Desmanthodium blepharodon* is known to me only by the description and by an illustration in Aristeguieta (1964). It does appear very close to *D. guatemalense* but is maintained here because of its geographical isolation and because of its thicker, basally ciliate leaves.

EXCLUDED SPECIES

Desmanthodium trianae Hieron. = *Clibadium trianae* (Hieron.) S.F. Blake, Contr. Gray Herb., n. ser. 52:6. 1917.

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RECOGNITION OF TRIBES CAPSICEAE AND PHYSALEAE, SUBFAMILY SOLANOIDEAE, SOLANACEAE

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ABSTRACT

Two new tribes in Solanaceae are described to accommodate new systematic information about the family. **Capsiceae** is centered on *Capsicum* and related genera, while **Physaleae** is centered on *Physalis* and related genera

KEY WORDS: Solanaceae, Capsiceae, Physaleae, Solanoideae, taxonomy

The genera *Capsicum* L. and *Physalis* L., family Solanaceae, subfamily Solanoideae, have traditionally been placed in tribe Solaneae (Wettstein 1891). They are distanced from *Solanum* L. (type species of the family and of the Solaneae) and most other members of the tribe by distinctive calyces and other features, and the following recognizes their distinctiveness at the tribal level.

Capsiceae D'Arcy, *tribus nov.* Type genus: *Capsicum* L., *Gen. Pl.*, ed. 5:86. 1754.

Herbae perennes vel frutices. Flores campanulati vel rotati. Calyces truncati, interdum dentes subapicales ferenti. Fructus baccati vel drupacei.

The calyx in *Capsicum* lacks the terminal lobes found in other Solanaceae but is apically truncate, sometimes with subapical enations that may resemble terminal lobes. The calyx is hardly accrescent in fruit. In his revision of *Lycianthes*, Bitter (1920) suggested a close relationship between *Lycianthes* and *Capsicum*, and subsequent morphological studies of the diagnostic calyces (D'Arcy 1986; Bernardello & Hunziker 1987) support this, arguing that these two genera form a core group of the new tribe Capsiceae. D'Arcy (1991) suggested that the following genera have calyx features at least superficially similar to *Capsicum* and may also belong to this new

tribe: *Acnistus*, *Aureliana*, *Dunalia*, *Iochroma*, *Lycianthes*, *Saracha*, *Tubocapsicum*, *Vassobia*, and *Witheringia*.

Physaleae D'Arcy, *tribus nov.* Type genus: *Physalis* L., *Gen. Pl.*, ed. 5: 85. 1754.

Herbae perennes vel frutices. Flores campanulati vel rotati. Calyces dentes terminales ferenti in statu fructu accrescenti. Fructus baccati vel drupacei.

The calyx in *Physalis* has terminal lobes and is accrescent in fruit, surrounding the berry. Anthers are longitudinally dehiscent, ovaries have nectaries, and plants never have prickles. In *Solanum*, calyces are only exceptionally accrescent (*S. sisymbriifolium* Lam., *S. toliarea* D'Arcy & Rakotozafy), anthers are poricidal, ovaries lack nectaries, and plants are often prickly, a suite of characters indicating more than a generic taxonomic distance.

Accrescent calyces occur in some other genera of Solanoideae, (e.g., *Witheringia folliculoides* J.L. Gentry & D'Arcy and *Nicandra physaloides* [L.] Gaertner). This suggests that accrescent calyces may be plesiomorphic in subfamily Solanoideae, appearing as a conservative condition in a few groups, or contrarily that accrescent calyces have risen independently in each of these lineages. In either case, accrescent calyces remain a single useful character to suggest the inclusion of *Physalis* and other genera in the new tribe, Physaleae. The following genera, which have similar accrescent calyces, are sometimes referred to as the 'physaloid group' and were suggested by Averett (1977, 1979), D'Arcy (1991) or Axelius (1996) to be closely allied to *Physalis*. They may also belong to this new tribe: *Archiphysalis*, *Brachistus*, *Chamaesaracha*, *Deprea*, *Jaltomata*, *Leucophysalis*, *Margaranthus*, *Mellissia*, *Quincula*, *Physaliastrum*, and *Withania*.

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A NEW SPECIES OF *ROLDANA* (SENECIONEAE) FROM OAXACA, MEXICO

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ABSTRACT

A new species, *Roldana calzadana* B.L. Turner, is described and illustrated from Oaxaca, México. It is closely related to the recently described *Senecio galicianus* McVaugh var. *manantlanensis* Kowal, which is endemic to the Sierra Manantlán of Jalisco. The latter is elevated to specific rank and treated as belonging to the genus *Roldana*, thus necessitating the following name change: *Roldana manantlanensis* (Kowal) B.L. Turner, *stat. & comb. nov.* In addition, the following new combinations within *Roldana* are proposed: *R. gonzalezae* (B.L. Turner) B.L. Turner, *comb. nov.*; *R. neogibsonii* (B.L. Turner) B.L. Turner, *comb. nov.*; and *R. sundbergii* (B.L. Turner) B.L. Turner, *comb. nov.*

KEY WORDS: Asteraceae, Senecioneae, México, Oaxaca, *Senecio*, *Roldana*, systematics

Studies on the Asteraceae of México have necessitated the following descriptions and name changes.

ROLDANA CALZADANA B.L. Turner, *spec. nov.* Figure 1. TYPE: MEXICO. Oaxaca: Mpio. San Martin Peras, carretera Coicoyan de las Flores - Santiago Juxtlahuaca (17° 17' N × 98° 11' W), "200 m de la deviacion a San Martin Peras", pine-oak woodland, ca. 2535 m, 16 Feb 1995, J.I. Calzada 19738 (HOLOTYPE: TEX!; Isotype: MEXU).

Similis *Roldanae manantlanensis* (Kowal) B.L. Turner sed habens folis graciliora, lobis deltationibus et irregulariter dentatis.



Figure 1. *Roldana calzadana*, from holotype.

Suffruticose herbs to 2 m high. Stems (upper) tawny-puberulous, pithy. Leaves (larger) 30-35 cm long, 16-20 cm wide; petioles 12-15 cm long; blades broadly ovate-elliptic in outline, cordate basally, 7-9 palmately nervate from the base, both surfaces glabrous, except along the major veins, the lateral margins bearing 5-6 deltoid lobes, each of the latter irregularly serrate. Heads arranged in rather flat-topped congested cymes ca. 6 cm high, 9 cm wide, the ultimate peduncles sparsely tomentose, 4-10 mm long. Involucres cylindro-campanulate, 5-6 mm high. Involucral bracts ca. 8, their apices greenish and broadly deltoid. Ray florets 3 per head; ligules yellow, 4-6 mm long, 1.5-2.5 mm wide; tubes puberulent. Disk florets 5 per head; corollas yellow, 7-8 mm long, sparsely pubescent. Achenes (immature) columnar, ca. 2 mm long, glabrous. Pappus of numerous readily deciduous white bristles 5-6 mm long.

This taxon is closely related to the recently described *Senecio galicianus* McVaugh var. *manantlanensis* Kowal, from Sierra Manantlán, Jalisco (*cf.* below). They possess similar habits, leaves and involucres, and both have similar florets with pubescent corollas. *Roldana calzadana* differs in having leaves with more broadly deltoid marginal lobes, each irregularly serrate, and heads arranged in rather congested flat-topped cymes which are over-topped by the upper foliage.

In my preliminary treatment of the *Roldana* complex for the comps of México (*cf.* Turner 1996), Barkley (in our collaborative work on *Senecio*, s.l.) prevailed upon me to treat *Roldana* within the broad bounds of his concept of *Senecio* (Barkley 1985); more recently he has come full circle and would treat *Roldana* (among many other segregates) as generically distinct. This has necessitated the following name changes:

ROLDANA GONZALEZAE (B.L. Turner) B.L. Turner, *comb. nov.* Based upon *Senecio gonzalezae* B.L. Turner, *Phytologia* 57:377. 1985.

ROLDANA NEOGIBSONII (B.L. Turner) B.L. Turner, *comb. nov.* Based upon *Senecio neogibsonii* B.L. Turner, *Brittonia* 37:119. 1985.

ROLDANA SUNDBERGII (B.L. Turner) B.L. Turner, *comb. nov.* Based upon *Senecio sundbergii* B.L. Turner, *Brittonia* 37:117. 1985.

ROLDANA MANANTLANENSIS (Kowal) B.L. Turner, *comb. & stat. nov.* Based upon *Senecio galicianus* McVaugh var. *manantlanensis* Kowal, *Brittonia* 43:109. 1991.

Kowal (1991) has provided a tedious, detailed, wonderfully elaborated upon, account documenting the biological reality of this taxon. He treats it as a variety of *Senecio galicianus* McVaugh but I think it deserving of specific rank and will recognize it as such in my treatment of *Roldana* for the *Comps of Mexico* (vol, 7, in prep).

Jeffrey (1992) transferred several other of my roldanoid species of *Senecio* into *Roldana*: these include *Senecio carlomansonii* B.L. Turner & T. Barkley; *S.*

gesneriifolius B.L. Turner 1987 (non *S. gesneriifolius* Cuatrec. 1950), but graciously given the new name *R. gesneriifolius* C. Jeffrey; *S. grimesii* B.L. Turner; *S. marquesii* B.L. Turner; *S. metapecus* B.L. Turner; and *S. nesomiorum* B.L. Turner.

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**COMMENTS ON THE DISTRIBUTION OF *BOTRYCHIUM LUNARIOIDES*
(OPHIOGLOSSACEAE) IN TEXAS**

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ABSTRACT

Botrychium lunarioides (Michx.) Sw. (Ophioglossaceae) is now known to be widespread and abundant throughout the eastern portion of Texas.

KEY WORDS: Ophioglossaceae, *Botrychium*, Texas, biogeography

Until recently, *Botrychium lunarioides* (Michx.) Sw. (Ophioglossaceae) was considered to be a species of the coastal plain of the southeastern United States whose westernmost distribution was known to extend to extreme east Texas (Thomas 1979; Thomas, *et al.* 1981; Wagner & Wagner 1993). In 1996, Do, *et al.* reported ten additional county records in the central portion of the Post Oak Savannah of Texas, thereby extending the known distribution of the species up to 273 km to the west. Additional field studies during 1996 have yielded nineteen new county records for the species in Texas (Figure 1). These new reports are primarily from the Post Oak Savannah, Pineywoods, and Blackland Prairies of northeast Texas and from the southern portion of the Post Oak Savannah. The most notable occurrence of the species is at Lake Bastrop State Recreation Area, Bastrop County, about 45 km ESE of Austin, which extends both the western and southern known limits of the species. The present distribution confirms that the plant is much more widespread and abundant within the state than previously known and that it may be expected to occur in nearly all counties of the Pineywoods and the Post Oak Savannah. Although the habitat of the very southern portion of the Post Oak Savannah (Caldwell, Gonzalez, Guadalupe, and Wilson counties), seems to be favorable for the species, an attempt to locate it

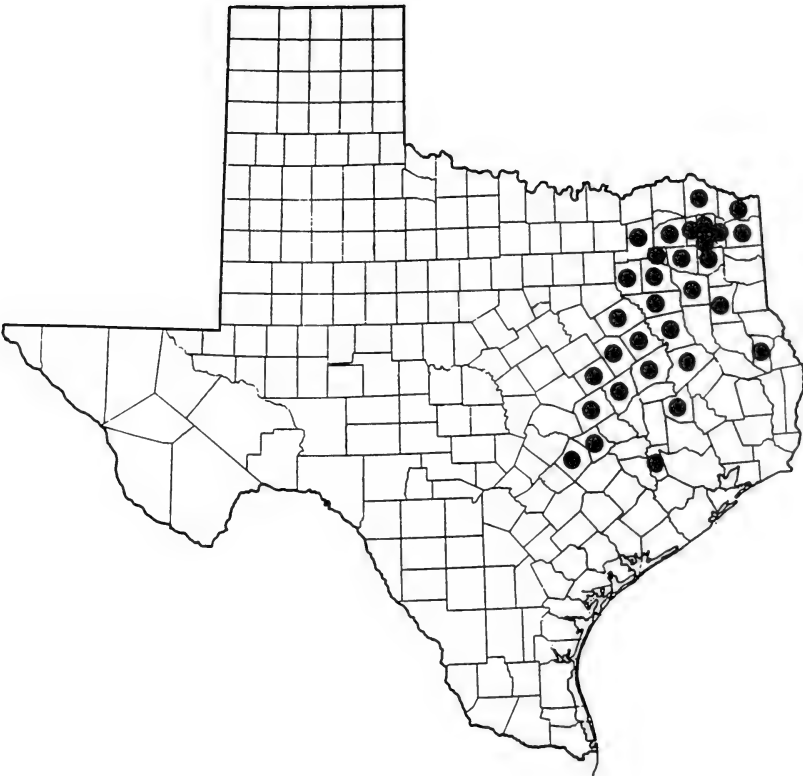


Figure 1. Documented distribution of *Botrychium lunarioides* in Texas.

there was unsuccessful. This failure may be related to the extreme drought in that area in the late winter and early spring of 1996, which has been mentioned by Thomas, *et al.* (1981) as a factor that may cause the species to remain dormant.

Specimens Examined: Texas: Anderson Co.: Cedar Creek Cemetery, between Long Lake and Elkhart on Texas Hwy. 294, 135 m, 14 Mar 1995, *Holmes 7602* (BAYLU). Bastrop Co.: Lake Bastrop State Recreation Area, ca. 0.6 mile S of jct. of FM 1441 and N Shore Park Road, lawn NE of boat ramp, 13 Mar 1996, *Singhurst 4806* (BAYLU). Bowie Co.: ca. 2.6 miles E of jct. of U.S. Hwy. 67 and FM 98 at Simms, Old Martin Cemetery, 6 Mar 1996, *Singhurst 4805* (BAYLU). Camp Co.: Rose Hill Cemetery, Tex. Hwy. 11 at jct. with U.S. Hwy. 271, 5 Apr 1996, *Stevens 203 & Gooch* (BAYLU). Cass Co.: Smyrna Cemetery on east side of Tex. Hwy. 77, ca. 4 miles NW of the Louisiana State line NW of Rodessa, LA and SW of Atlanta, TX, 31 Mar 1988, *Thomas 103695, Dorris, & Slaughter* (NLU). Franklin Co.: Hogansport Cemetery on County Road NW 1028 ca. 0.1 mile S of FR 71, 5 Apr 1996, *Stevens 200 & Gooch* (BAYLU). Freestone Co.: Fairfield Lake State Recreation Area, 6 miles NE of Fairfield, Chancellor Cemetery, 22 Feb 1995, *Do 324* (BAYLU); New Hope Cemetery, 18 Mar 1995, *Singhurst 3029* (BAYLU). Falls Co.: Williams Cemetery, ca. 5 miles S of Kosse on Texas Hwy. 14, 17 Mar 1995, *Singhurst 3004* (BAYLU). Henderson Co.: Ash Cemetery, just SE of Murchison on Tex. Hwy. 31, 17 Mar 1995, *Holmes 7610* (BAYLU). Hopkins Co.: Harmony Cemetery on County Road 2397 ca. 0.5 miles NW of County Road 2403, 5 Apr 1996, *Stevens 206 & Gooch* (BAYLU). Houston Co.: ca. 0.2 mile N of jct. Tex. Hwy. 21 and park road, ca. 5 miles NW of L.R. Price Log Cabin; 29 Jan 1996, *Singhurst 4734* (BAYLU). Hunt Co.: Donelton Cemetery on County Road 3219 ca. 0.8 mile NW of FR 1567, 6 Apr 1996, *Stevens 208 & Gooch* (BAYLU). Kaufman Co.: New Salem Cemetery on County Road 315 ca. 1.5 miles N of Interstate Hwy. 20, 6 Apr 1996, *Stevens 210 & Gooch* (BAYLU). Lee Co.: Tanglewood Cemetery, ca. 5.2 miles N of jct. of U.S. Hwy. 77 and FM 696, ca. 0.2 mile W and N on unnamed road ca. 0.4 mile, 31 Jan 1996, *Singhurst 4773* (BAYLU). Leon Co.: FR 3, 1.5 miles S of jct. with U.S. Hwy. 79 at Winn Cemetery, 110 m, 3 Mar 1995, *Gooch 63, Stevens, & Holmes* (BAYLU). Limestone Co.: McKenzie Cemetery, 12 Mar 1995, *Singhurst 3024* (BAYLU); Cobb Cemetery, 12 Mar 1995, *Singhurst 3024* (BAYLU); Cobb Cemetery, 12 Mar 1995, *Singhurst 3025* (BAYLU); Ferguson Cemetery, off FR 937, ca. 2 miles NW of the Robertson Co. line, 12 Mar 1995, *Singhurst 3020* (BAYLU). Milam Co.: Old Providence Cemetery, 20 Mar 1995, *Singhurst 3201* (ASTC). Morris Co.: Daingerfield State Park, ca. 2.1 miles S of jct. of Tex. Hwy. 49 and park road, lawn area ca. 80 m NW of activity center, 7 Mar 1996, *Singhurst 4801* (BAYLU). Navarro Co.: Midway Cemetery, ca. 7 miles NE of Streetman, 18 Mar 1995, *Singhurst 3028* (BAYLU). Rains Co.: Prospect Cemetery on County Road 1230 ca. 0.5 mile S of U.S. Hwy. 69, 6 Apr 1996, *Stevens 209 & Gooch* (BAYLU). Red River Co.: McCrary Cemetery on FR 196 ca. 2 miles W of Tex. Hwy. 37, 5 Apr 1996, *Stevens 198 & Gooch* (BAYLU). Robertson Co.: FR 979 at jct. with FR 2096 at Bald Prairie Cemetery, 98 m, 3 Mar 1995, *Stevens 82, Gooch, & Holmes* (BAYLU); Seale Round Prairie Cemetery, off FR 937, ca. 2 miles SE of the Limestone Co. line, 12 Mar 1995, *Singhurst 3022* (BAYLU). Rusk Co.: Martin Creek State Park, ca. 1.3 miles SW of jct. of FM 1716 and park road, lawn next to cabin no. 1, 5 Mar 1996, *Singhurst 4804* (BAYLU). San Augustine Co.: Liberty Hill Baptist Church Cemetery, 2.3 miles N of Tex. Hwy. 21 by Tex. Hwy. 147, 16 Feb 1972, *Thomas 27495* (NLU). Smith Co.: Tyler State Park, 0.6 mile W

of jct. of FR 14 and park road, lawn S of registration office, 4 Mar 1996, *Singhurst 4803* (BAYLU). Titus Co.: Winfield Cemetery on Interstate Hwy. 30 ca. 200 m E of Spur 185, 5 Apr 1996, *Stevens 201 & Gooch* (BAYLU). Upshur Co.: Cemetery on U.S. Hwy. 271 ca. 1 mile S of Camp Co. line, 5 Apr 1996, *Stevens 204 & Gooch* (BAYLU). Van Zandt Co.: Purts Creek State Recreation Area, at jct. of FM 316 and Gosham Road, 4 May 1995, *Singhurst 3261* (BAYLU). Walker Co.: Huntsville State Park, jct. of Interstate Hwy. 45 and park road, ca. 1.9 miles SW of park road, N side of park road in lawn E of education center, 28 Feb 1996, *Singhurst 4800* (BAYLU). Waller Co.: Macedonia Cemetery, E off of Macedonia School Road, N of Magnolia Road and S of Threemile Creek near the intersection of Harris, Walker and Montgomery cos., 19 Mar 1992, *Brown 15832* (BAYLU (photo), SBSC). Wood Co.: Perryville Cemetery on FR 852 ca. 0.5 mile S of FR 1647, 5 Apr 1996, *Stevens 205 & Gooch* (BAYLU).

ACKNOWLEDGMENTS

We wish to thank Larry E. Brown of SBSC for the loan of a specimen from Waller County, the Texas Parks and Wildlife Department for access to public lands under their jurisdiction, and the Beta Tau Chapter of Beta Beta Beta of Baylor University for partial financial support provided through a Bob Gardner Memorial research Grant to Stevens and Gooch.

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NEW COMBINATIONS FOR THE FLORA OF THE CENTRAL EASTERN
UNITED STATES

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ABSTRACT

New combinations are made for *Panicum acuminatum* var. *wrightianum* and *P. sphaerocarpon* var. *isophyllum*.

KEY WORDS: Poaceae, *Panicum*, Eastern United States, nomenclature

The following new combinations are necessary for the completion of a manuscript for the Flora of the Central Eastern United States.

1. *Panicum acuminatum* Swartz var. *wrightianum* (Scribn.) Reed, *comb. nov.*
BASIONYM: *Panicum wrightianum* Scribn., U.S.D.A., Div. Agrost. Bull. 11:44, f. 4. 1898.
2. *Panicum sphaerocarpon* Elliott var. *isophyllum* (Scribn.) Reed, *comb. nov.*
BASIONYM: *Panicum microcarpon* Muhl. var. *isophyllum* Scribn., Bull. Tenn. Agric. Exp. Sta. 7:51, f. 54. 1894.

A NEW SPECIES OF *GALIUM* (RUBIACEAE) FROM NORTHEASTERN MEXICO

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ABSTRACT

Galium hintoniorum B.L. Turner, *spec. nov.*, is described and illustrated. It is a prostrate rhizomatous herb with numerous relatively small leaves and is known only from southernmost Tamaulipas, México, where it occurs in oak woodlands between 1300 and 1900 meters.

KEY WORDS: Rubiaceae, *Galium*, México, Tamaulipas, systematics

Routine identification of plants from the Sierra Madre Oriental of northeastern Mexico has revealed the following novelty.

GALIUM HINTONIORUM B.L. Turner, *spec. nov.* Figure 1. TYPE: MEXICO. Tamaulipas: Mpio. Guemes, Los Pedros, "Grass savannah in oak woods," 1355 m, 10 Nov 1994, *Hinton, et al.* 25127 (HOLOTYPE: TEX!).

Simile *G. microphylo* A. Gray sed foliis plerumque parvioribus, nigrescentibus in sicco (vice viridium), apicibus foliorum tantum acutatis (vice apicum apiculatum), et fructificationibus pubescentibus (vice glabrarum) cum pilis parvis arcuatisque.

Prostrate rhizomatous herbs 10 cm high or less. Stems moderately white-pilose with spreading hairs to densely ciliate with upcurved arcuate hairs, the vestiture 0.1-0.3 mm high. Leaves 4 to a node throughout, numerous and much overlapping; petioles ca. 0.25 mm long; blades ovate-elliptic to narrowly oblanceolate, mostly 3-9 mm long, 1-2 mm wide, uninervate, glabrous or nearly so, shiny, the margins entire and thickened, the apices merely acute. Flowers few, mostly axillary and shortly pedicellate but some of them seemingly terminal and sessile. Flowers rotate campanulate, the petals 2-3 mm long, glabrous. Fruiting bodies ca. 1.2 mm long, moderately and evenly ornate with arcuate upcurved hairs.

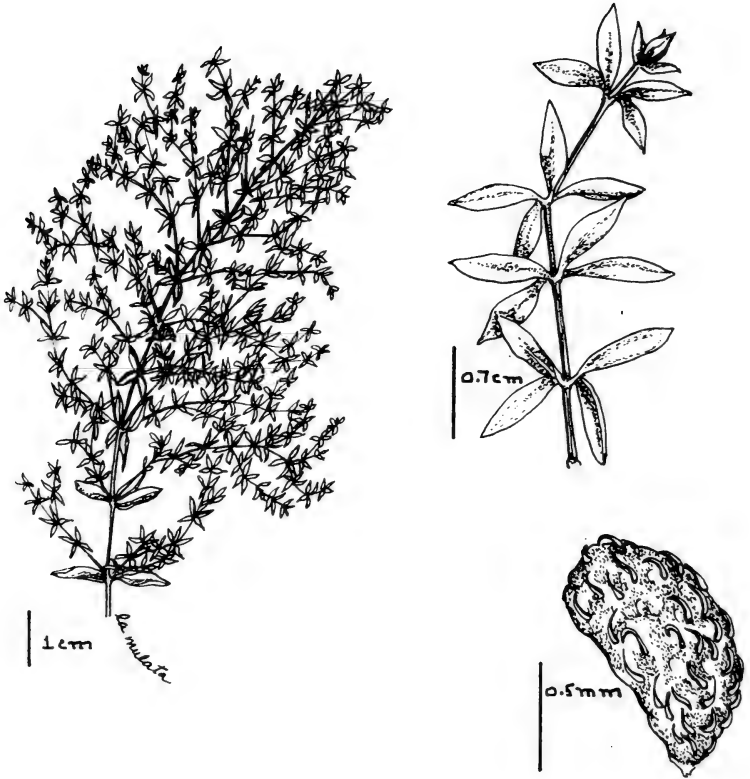


Figure 1. *Galium hintoniolum*, from holotype; upper right, portion of midstem showing leaves; lower right, fruiting body.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. Tamaulipas: Mpio. Hidalgo, Los Caballos, 1705 m, 21 Sep 1994, *Hinton, et al.* 24804 (TEX); road from Sta. Engracia toward Dulces Nombres, N.L., 0.3 mi W of Paraje de Los Caballos (22° 58' 39" N × 99° 29' 31" W), 1840 m, 21 Sep 1994, *Nesom* 7460 with Jaime Hinton & M. Mayfield) (TEX).

Galium hintoniorum much resembles *G. microphyllum* but it apparently lacks the 4-bracted flowers of that taxon, and the fruits are ornamented with recurved hairs, as illustrated in Figure 1. Additionally, the foliage dries black and is more densely packed, the leaves lacking whip-like acuminations at their apices as occur in *G. microphyllum*.

In short, the species appears to stand somewhere between the *Relubium* taxa (*Galium microphyllum*, et al.) and the more typical elements of *Galium*, seemingly vitiating the characters upon which these two genera are founded.

The species is named for the Hinton family, all of the collections having been made by or with Jaime Hinton, the extant patriarch of that remarkable clan.

ACKNOWLEDGMENTS

I am grateful to Gayle Turner for the Latin diagnosis, and to her and Ted Delevoryas for reviewing the manuscript. Maria Thompson provided the illustration.

NOMENCLATRURAL COMBINATIONS IN *CYPERUS* (CYPERACEAE)

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ABSTRACT

The following nomenclatural changes in Cyperaceae are proposed: *Cyperus macrocephalus* F. Liebmann var. *eggersii* (J. Böckeler) *comb. nov.*; *Cyperus odoratus* C. Linnaeus var. *engelmannii* (E. von Steudel) *comb. et stat. nov.*; and *Cyperus odoratus* C. Linnaeus var. *squarrosus* (J. Böckeler) *comb. nov.*

KEY WORDS: Cyperaceae, *Cyperus*, nomenclature, *Cyperus eggersii*, *Cyperus macrocephalus*, *Cyperus odoratus* var. *engelmannii*, *Cyperus odoratus* var. *squarrosus*, subgenus *Dictidium*

Tucker (1994) treated *Cyperus eggersii* J. Böckeler as a synonym of *C. odoratus* C. Linnaeus, subgenus *Dictidium* (Nees von Esenbeck) C.B. Clarke [Sy = subgenus *Torulinium* (N. Desvaux) G. Kükenenthal]. Adams (1991, 1994) recognized subgenus *Torulinium* at the rank of genus and placed *Cyperus eggersii* as a variety of *Torulinium macrocephalum* (F. Liebmann) C.B. Clarke. We agree with Tucker's placement of subgenus *Dictidium* (Sy = *Torulinium*) but agree with Adams that *Cyperus eggersii* should be recognized as a variety of *C. macrocephalus* F. Liebmann. However, since Adams recognized subgenus *Torulinium* as a distinct genus, a new combination in *Cyperus* becomes necessary. We have examined herbarium specimens and field populations of all three taxa from Texas south to Belize. We have found but a single population appearing as a putative hybrid between *C. eggersii* and *C. ferruginescens* J. Böckeler and have had no problems differentiating one taxon from another. This is not to say that somewhere, mixed populations and intermediates may exist. However, we have done extensive field and herbarium work and do not see the justification for treating these three taxa as a single entity.

Cyperus macrocephalus F. Liebmann var. ***eggersii*** (J. Böckeler) S.D. Jones, J. Wipff, & R. Carter, *comb. nov.* BASIONYM: *Cyperus eggersii* J. Böckeler, Beiträge zur Kenntniss der Cyperaceen 1:53. 1888. *Torulinium eggersii* (J. Böckeler) C.B. Clarke in I. Urban (Editor), *Symbolae Antillanae Seu Fundamenta Florae Indiae Occidentalis* 2:56. 1900-1901. *Torulinium macrocephalum* (F. Liebmann) T. Koyama var. *eggersii* (J. Böckeler) C.D. Adams, Annals of the Missouri Botanical Garden 78:254. 1991. TYPUS: REPUBLICA DOMINICANA. Santo Domingo: near Batey on Río Yasica, 23 Jun 1887, Eggers 2627 (HOLOTYPE: B).

Many North American authors since Fernald (1950) have treated *Cyperus engelmannii* E. von Steudel and *C. ferruginescens* J. Böckeler as synonyms of *C. odoratus*, usually without explanation. Two notable exceptions are Braun 1967 and Voss 1972. Most authors refer to *C. odoratus* as a polymorphic species commenting that *C. odoratus* is the most variable *Cyperus* in their area. We find these three taxa closely related and mostly sympatric, but discrete. Although some intermediates exist, they are relatively few. Considering their distinct morphologies, we believe that varietal rank under *C. odoratus* is warranted for *C. engelmannii* and *C. ferruginescens*. The following combinations are made:

Cyperus odoratus C. Linnaeus var. ***engelmannii*** (E. von Steudel) R. Carter, S.D. Jones, & J. Wipff, *comb. et stat. nov.* BASIONYM: *Cyperus engelmannii* E. von Steudel, *Synopsis Plantarum Cyperacearum* 2:47. 1854. *Cyperus ferax* L.C. Richard subsp. *engelmannii* (E. von Steudel) G. Kükenenthal, Pflanzenreich 4(20):620. 1936. TYPUS: UNITED STATES. Illinois: Cahokia, Sep 1845, G. Engelmann s.n. (HOLOTYPE: P?; Isotype: GH).

Cyperus odoratus C. Linnaeus var. ***squarrosus*** (N. Britton) S.D. Jones, J. Wipff, & R. Carter, *comb. nov.* BASIONYM: *Cyperus speciosus* M.H. Vahl var. *squarrosus* N. Britton, Memoirs of the Torrey Botanical Club 13:214. 1886. *Cyperus ferruginescens* J. Böckeler, Linnaea. 36:396-397. 1869-70. *Cyperus speciosus* M.H. Vahl var. *ferruginescens* (J. Böckeler) N. Britton, Memoirs of the Torrey Botanical Club 5:61. 1894. TYPUS: UNITED STATES. Missouri: St. Louis. No specimen cited in protologue.

The following key is modified from O'Neill (1940) and will differentiate the species of *Cyperus* subgenus *Dictidium* in Texas.

KEY TO *CYPERUS* SUBGENUS *DICLIDIUM* IN TEXAS

1. Inflorescence consisting of a single aggregated subglobose head, the spikes sessile; in Texas, restricted to the Lower Rio Grande Valley and sparingly upward along the coast to the Coastal Bend. *C. macrocephalus* var. *macrocephalus*
1. Inflorescence consisting of several peduncled spikes.

2. Spikelets appressed to ascending, densely crowded; in Texas, restricted to the Lower Rio Grande Valley. *C. macrocephalus* var. *eggersii*
2. Spikelets divaricate, scattered along the rachis of the spike; in Texas, widely distributed.
3. Scales near the middle of the spikelet (2.7-)2.8-3.2 mm long; rachilla wings reaching or covering the shoulders of the achene; achenes (1.2-)1.3-1.5 mm long, (0.5-)0.6-0.7 mm wide; spikelets brownish. *C. odoratus* var. *odoratus*
3. Scales near the middle of the spikelet (2.0-)2.3-2.5(-2.6) mm long, rachilla wings rarely reaching and never covering the shoulders of the achene; achenes 0.8-1.0(-1.1) mm long, (0.3-)0.4-0.5 mm wide; spikelets reddish.
4. Tip of scale reaching only to base of the scale next above and on the same side of the rachis. *C. odoratus* var. *engelmannii*
4. Tip of scale conspicuously reaching over the base of the scale next above on the same side of the rachis. *C. odoratus* var. *squarrosus*

ACKNOWLEDGMENTS

We appreciate Paul A. Fryxell (TEX) and Gretchen D. Jones (USDA-ARS) for their manuscript review. We thank Dan Nicolson (Smithsonian) for his constructive comments on selected nomenclature.

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A NEW VARIETY OF *COREOPSIS MUTICA* (ASTERACEAE) FROM
WESTERN OAXACA

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ABSTRACT

A new variety of *Coreopsis mutica*, *C. mutica* var. *miahuatlana* B.L. Turner, is described from Mpio. Miahuatlán, Oaxaca, México. It is a shrub or small tree 2.0-5.0 m high and relates closely to var. *subvillosa*. The distinctions between these two varieties are discussed.

KEY WORDS: Asteraceae, *Coreopsis*, México, Oaxaca, systematics

Crawford (1970) provided an excellent study of *Coreopsis mutica* A. DC. in which seven regional varieties were recognized. Crawford (1981) added an additional varietal element to the group. Turner (1992) reviewed the taxonomy of the complex, reducing some of Crawford's taxa to synonymy, but added a newly described taxon, *C. mutica* var. *guerreroana* B.L. Turner, maintaining seven varietal taxa, all of these keyed and mapped.

I describe herein a new variety, *Coreopsis mutica* var. *miahuatlana* from west-central Oaxaca, where it is seemingly confined to Mpio. Miahuatlán. In my revised key to the group (Turner 1992) the present taxon will key to var. *carnosifolia* D. Crawford, but differs from the latter in having much larger, less succulent leaves which dry dark (vs. semisucculent smaller leaves which dry pale green). In addition the capitulescence is broader and more numerous-headed. The closest relationship of var. *miahuatlana* appears to be with var. *subvillosa* D. Crawford; indeed, occasional specimens of the former take on characters of the latter (e.g., *Hinton* 26603, in pubescence; and *Hinton* 26735, in its lobed leaves). In my treatment of 1992 I included at least one collection of var. *miahuatlana* (Turner 80A-9 [TEX], cited below) in my concept of var. *subvillosa*, taking this at the time to be an intermediate between var. *subvillosa* and var. *carnosifolia*. I would now call this collection an intergradant between the latter and var. *miahuatlana*.



Figure 1. *Coreopsis mutica* var. *miahuatlana* (from holotype).

COREOPSIS MUTICA A. DC. var. **MIAHUATLANA** B.L. Turner, var. nov.
Figure 1. TYPE: MEXICO. Oaxaca: Mpio. Miahuatlán, Santo Domingo, 2240 m, IRF Río Magdalena, tree 5 m, common, 4 Aug 1996, Hinton, et al. 26724 (HOLOTYPE: TEX!).

Similis *Coreopsi muticae* (*Coreopsis mutica*) A. DC. var. *subvillosa* D. Crawford, sed plantae majores sunt, foliis primariis majoribus, plerumque 10-13 cm longis (vice 3-9 cm longis), denigratis ubi siccis, glabris aut paene glabris ubique, et foliis immaturis subvillosis.

Shrub or small tree 2.0-5.0 m high. Stems and foliage glabrous throughout or nearly so, but juvenile leaves sometimes moderately to sparsely pubescent. Midstem (primary) leaves mostly 10-15 cm long, 2.5-4.5 cm wide, drying dark green or blackish, the margins serrulate. Heads numerous, arranged in broad rounded terminal corymbose panicles 5-10 cm high, 10-16 cm across. Primary peduncles 1-2 cm long, the ultimate peduncles mostly 1-3 cm long. Involucre narrowly campanulate, 7-9 mm high, 5-6 mm wide (pressed); outer bracts 4-5, oblanceolate, 3-nervate, mostly 4-7 mm long; inner bracts ca. 8, subscarious, free to base or nearly so. Ray florets mostly 5; ligules yellow, 1-2 cm long, 0.6-1.0 cm wide. Disk florets 18-25 (estimated); corollas yellow. Anther sacs purple. Achenes narrowly ellipsoidal, ca. 8 mm long, 2 mm wide.

ADDITIONAL SPECIMENS EXAMINED: (all from Mpio. Miahuatlán): Quiexobra, 2300 m, deep rocky gorge, 14 Oct 1995, Hinton, et al. 26122 (TEX); Xianaguilla, 2325 m, 22 Oct 1995, Hinton, et al. 26327 (TEX); above Xianaguilla, 2550 m, 23 Oct 1995, Hinton, et al. 26357 (TEX); San Francisco Ozolotepec, 2815 m, 8 Aug 1996, Hinton, et al. 26839 (TEX); 35 mi. SE of Ejutla, road to Puerto Angel, 22 Aug 1980, Turner 80A-9 (TEX).

All of the above collections are said to be common shrubs or trees, varying from 2.0-5.0 m high and collected between 2240-2815 m in pine-oak forests. The closest relative of var. *miahuatlana* is the allopatric var. *subvillosa*, which is consistently described as a suffrutescent herb or shrub 0.5-2.0 m high, occurring in pine-oak forests from 2100-2500 m.

In Crawford's (1970) treatment of the *Coreopsis mutica* complex, var. *miahuatlana*, because of its 5-6 ray florets, will key to or near *C. mutica* var. *microcephala* D. Crawford, a taxon with smaller heads occurring to the east of the Isthmus of Tehuantepec. I gave this identification to the first collections of the present plants obtained from the Miahuatlán area by James Hinton, but the fine series of subsequent collections obtained by this ardent field botanist has lead me to conclude that the taxon concerned is deserving of formal recognition.

ACKNOWLEDGMENTS

I am grateful to Gayle Turner for the Latin diagnosis, and to her and Justin Williams for reviewing the manuscript. Ms. Maria Thompson provided the illustration.

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NOMENCLATURAL CORRECTION IN *VIOLA* (VIOACEAE)

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ABSTRACT

Viola sororia Willd. var. *affinis* (Leconte) L.E. McKinney was incorrectly used as the basionym in a previously published combination to change this taxon to subspecific rank. This note corrects the previous combination.

KEY WORDS: *Viola*, Violaceae, nomenclature

Viola sororia Willd. var. *affinis* (Leconte) L.E. McKinney (McKinney 1992:39), was used incorrectly as the basionym to change this taxon to subspecific rank (Little 1992). The following nomenclatural change is made to correct this error and to achieve consistency with the treatments of Violaceae in the Jepson Manual Project and for the Vascular Plants of Arizona Project:

Viola sororia Willd. subsp. *affinis* (Leconte) R.J. Little, *stat. et comb. nov.*
BASIONYM: *Viola affinis* Leconte, Ann. Lyceum Nat. Hist. N.Y. 2:138. 1826.

ACKNOWLEDGMENTS

I thank Dr. Bruce Bartholomew of the Botany Department, California Academy of Sciences, Golden Gate Park, San Francisco, CA, for bringing to my attention the need to correct the basionym reference and for reviewing this note.

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NEW LOCATIONS AND INTERPRETATION OF VERNAL POOLS IN SOUTHERN CALIFORNIA

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ABSTRACT

An undocumented series of disturbed and remnant vernal pools was discovered during the abnormally wet 1992-1993 rainfall season in coastal southern California at San Clemente State Beach in southwestern Orange County, and from two sites at San Onofre State Beach in northwestern San Diego County. An additional series of remnant terrace vernal pools was found between Rancho Laguna and the City of San Clemente also in coastal Orange County. San Diego pools associated with either claypan or duripan soils have different suites of plant species despite their close proximity. The coastal Orange County pools, herein proposed as possible liquefaction-origin pools, also support a distinctive flora.

Aerial photographs of the region made prior to extensive urbanization show widespread fields of mima mounds (which coincide with present pool localities), likely indicating extensive historical vernal pool habitat. In coastal Orange County, remnant mima mound-type topography is present only at San Clemente State Beach and at Moulton Meadows in Laguna Beach; fragmented mounds occur in the Dana Hills and the City of San Clemente. We suggest that the origin of some mima mounds in coastal southern California may be attributed to Holocene seismic activity and liquefaction-related events. A biogenic maintenance hypothesis is proposed for the mima mounds: foraging activities by fossorial (burrowing) rodents in liquefaction terrain may play an important role in deterring long-term erosion of mounds and filling in of intermound pools. New word models are presented to explain how these relationships might have evolved including: "earthquake successional sequences" and "seismogenic tracker species." Earthquake successional sequences, including intermittent pools and mounds, provide habitat created by

ongoing seismic and liquefaction-related activities for invasion by seismogenic tracker organisms, which possibly include fairy shrimp, western spadefoot toad, pocket gophers, and other opportunistic species whose mode of life is in part associated with seismic-induced terrain.

We describe the previously unrecognized role of cryptogamic vegetation in regulating microscale gradients such as moisture status, nutrient availability, soil temperature, microbial processes, and safe-site seed selection which directly affect the biology of vernal pools. The cyanobacterium, *Microcoleus vaginatus*, is identified as a potential keystone organism occupying vernal pools and astatic alkaline sinks in southern and central California. A preliminary catalog of the cryptogamic and phanerogamic flora of vernal pools and adjacent upland terrain is presented. A number of rare or regionally uncommon vascular plants were collected during this study including *Atriplex pacifica*, *Dudleya blochmaniae*, and *Myosurus minimus*. New records documented for Orange County include the native *Trifolium variegatum* and the exotics *Atriplex lindleyi* and *Hainardia cylindrica*, *Glinus lotoides*, introduced from Europe, is new for San Diego County.

KEY WORDS: Vernal pools, California, Orange County liquefaction-origin pools, San Diego County duripan/claypan pools, fossorial rodents, mima mounds, Holocene earthquakes, seismogenic tracker species, cryptogamic crusts, *Microcoleus vaginatus*, keystone species, fairy shrimp

INTRODUCTION

California's vernal pools are small to medium sized temporary ponds which form above hardpan, claypan, or volcanic mudflow soils during the winter rain season but drain completely by late spring (Bauder 1986); vernal pools are often defined and identified by their endemic or regionally restricted flora (Thorne 1984). They range in size from a few square meters to several hectares and are always shallow, most by 10 to 60 centimeters (Zedler 1987). Pools larger than 20 hectares are referred to as vernal lakes (Holland 1976). Vernal pools are also surface water depression wetlands according to Novitzki (1979). Perched above an impermeable soil layer and separated from groundwater or stream channel inflow, a vernal pool fills only by slowly collecting precipitation, although the wet-life of vernal pools may be extended by subsurface flows (Hanes, *et al.* 1990). Although evaporation exceeds precipitation in most coastal southern California wetlands (Stevenson & Emery 1958), vernal pools also share characteristics of ombrotrophic (rainy) environments since precipitation-dominated wetlands receive nutrient inputs primarily from wet and dry atmospheric deposition (Doss 1995). Despite the recognized importance of hydrogeologic regimes in driving nutrient dynamics in wetlands (Carter 1986; Labaugh 1986), the relationship between hydrologic processes and nutrient cycling in vernal pools has not been addressed.

Zedler (1990) has likened the winter vernal pool habitat to a cool-temperate pond, and in late spring to autumn, a desert. Nestled within a subtle upland depression, the pool erratically fills and empties, often repeatedly throughout the season due to uncertain rainfall before completely drying by evapo-transpiration. The dry vernal

pool pan, also described as a dry marsh bed (Kopecko & Lathrop 1975), may persist for years without filling completely, especially during severe drought. Winter ponding deters most aggressive upland plants from invading a vernal pool; and in shallow pools, the relatively short-lived inundation period also slows development of the permanent anaerobic conditions necessary for establishment of many marshland species. The recurrent inflow of rainwater produces an ephemeral amphibious environment with micro-niches for vascular plant and cryptogamic species including an easily overlooked, shallow undulating pool margin that simulates a tidal mud flat. Alternating winter inundation and summer drought has selected a unique assemblage of amphibious plants and animals including specialized endemics as well as a group of aquatic generalists capable of tolerating a double-stress regime. Zedler (1990) developed the "recurrent gap" hypothesis based upon the reliable recurrence of microhabitats due to uncertain rainfall to explain traits in annual seed plants; accordingly, we emphasize the importance of the "recurrent flux" of inundating rainfall in the creation of niches for cryptogams in vernal pool terrain.

The floristic composition of a vernal pool may be perpetuated for decades because southern California's arid climate does not support peat formation, a process that speeds up plant community succession; the amphibious character of this habitat and its specialized biota are closely dependent on California's Mediterranean-type climate which is characterized by mild, moderately wet winters and rain-free summers. Zedler (1987) describes four stages of pool development: 1) a wetting phase; 2) an aquatic phase; 3) a drying phase; and 4) a drought or dormant phase. Vernal pool plants and animals often depend upon one or more of these specific phases (Zedler 1987; Holland & Jain 1984). Although Zedler (1987) indicates that climate is key for the establishment of true vernal pool habitat, edaphic factors may be more important with respect to the vegetation than climate (Holland & Dains 1990).

Vernal pools are not unique to California (Thorne 1984), but their plant communities of course are (Holland & Jain 1977). Intermittent pools and pool-forming processes that most closely simulate and support biota characteristic of California's vernal pools, occur primarily in other Mediterranean climate regions (*i.e.*, South Africa, southwestern Australia, the Mediterranean Basin, and Chile). Phytogeographic phenomena, including amphitropical disjunctions of the same or similar phanerogamic species between the pools of temperate North and South America, also link the vernal pool biota of the Mediterranean climate regions. Long-distance dispersal by migrating birds is probably involved (Raven 1963). Members of California's vernal pool flora which have disjunct austral counterparts include species of *Marsilea*, *Crassula*, *Isoetes*, *Myosurus*, and *Eryngium* (Zedler 1987). New information on the phytogeography of cryptogamic vegetation suggests that species shared between southern California and other Mediterranean climates may be relicts of an ancient Madro-Tethyan flora rather than products of long-distance dispersal, which is less likely for many lichens and bryophytes. The cryptogamic flora of South Africa and California, unlike the vascular flora, does share identical and vicariant taxa, *i.e.*, *Buellia halonia* (Ach.) Tuck., *Punctelia punctilla* (Hale) Krog, and *Trichoramalina crinitum* (Tuck.) Rundel & Bowler/*T. melanothrix* (Laur.) Rundel & Bowler (Bowler & Rundel 1974; Riefner 1989; Weber 1993). The recent discovery of *Ramalina canariensis* Steiner in California (Riefner & Bowler 1994), previously documented from all the Mediterranean climate regions except California, points to our lack of understanding of dispersal mechanisms and relict endemism on the continental level.

Additional study may yet link the cryptogamic vegetation of California's vernal pools with that of other Mediterranean climates.

Vernal pools and much of their biota are considered to be the most specialized and endangered type of wetland in California (Bauder 1986; Cheatham 1976; Cochrane 1985; Ferren & Pritchett 1988; Ferren & Fiedler 1993; Holland & Griggs 1976; Thorne 1984; Zedler 1987). The rigors of the habitat have provided fertile ground for rapid evolutionary radiation in the vascular flora (Stone 1990). Noteworthy are several characteristic genera of annual plants including *Downingia*, *Eryngium*, *Lasthenia*, *Limnanthes*, *Navarretia*, *Orcuttia*, *Plagiobothrys*, and *Pogogyne*. Many taxa often belong to a suite of narrowly restricted species which occupy a particular pool type characterized by specific soil properties, inundation regimes, and/or elevation (Bauder 1993). The likelihood that a particular suite of species is present in any one pool group is determined by a highly localized set of gradients that may not be widely encountered. Bauder (1993) has discussed differences in microscale gradients of soil and elevation affecting vernal pool plants in San Diego County, including highly localized species such as *Pogogyne abramsii* J.T. Howell and *Downingia concolor* E. Greene subsp. *brevior* McVaugh. Similar evidence documenting the microscale conditions of soils and inundation regimes for specific suites of species in Merced and Placer counties was presented by Holland & Jain (1990). Selective pressures exerted by multiple local and microscale parameters including soils, inundation regimes, temperature, and factors such as fungal associates which may affect germination have contributed to the complexity of vernal pool ecology and evolution.

Holland & Jain (1990) believe that floras of vernal pools differ according to soil type, while Bauder (1987) and Zedler (1987) state that local pool composition and structure in southern California are best explained by frequency and duration of ponding. We believe a more intricate web of functionally linked physical-hydrogeologic and biological processes including local hydrologic cycles and climate patterns, landform age and origin of mound-depression microrelief, nutrient cycling, microbiota and cryptogamic vegetation, abiotic and biotic factors which maintain mound-depression terrain, site history, and disturbance all interact to affect the diversity and abundance of plants and other organisms in southern California's vernal pool terrain.

Vernal pools occur within an upland vegetation matrix of grassland, chaparral, coastal sage scrub, and/or oak woodland habitat. Because of their isolation, vernal pools have frequently been referred to as terrestrial or ecological islands (Holland & Jain 1988; Zedler 1987; Schoenherr 1992; Stone 1990). The quasi-endemic nature of vernal pool "island plants" is due in part to lack of seed dispersal mechanisms which favors keeping the seed supply on-site. Zedler (1990) compiled data indicating that nearly three-quarters of the vernal pool species in San Diego County have no obvious means of dispersal. Clusters of "island" pools have been referred to as archipelagoes, suggesting that principals of island biogeography might be used to unravel complex phytosociological patterns correlated with pool numbers and size (Holland & Jain 1981, 1988).

In this paper, we refer to local patches of remnant pool habitat as islands within an upland vegetation matrix, and to chains of such patches as archipelagoes (Burkey 1995). Herein, we report new localities of San Diego claypan and duripan vernal pool

habitat and a new archipelago comprised of the previously uncharacterized Orange County vernal pools. The San Diego and Orange county pools each support different suites of plant species. The ready accessibility of these pools with their distinctive floras offers a rare opportunity to study the complex, and still incompletely known, biotic interactions within vernal pool communities.

DISTRIBUTION OF CALIFORNIA VERNAL POOLS

In western North America, vernal pools have been reported from southern Oregon southward into Baja California, México (Holland & Griggs 1976; Kagan 1986; Moran 1984). The vernal pools of California primarily occur in two clusters: 1) the coastal terraces and areas of gentle topography of the lower coastal mountains from Sonoma to San Diego County; and 2) from Shasta to Kern county in the Central Valley (Zedler 1987; Holland & Jain 1977; Ferren & Pritchett 1988). Vernal pool vegetation is best developed in the eastern Central Valley on ancient terrace soils bordering the foothills of the Sierra Nevada, where concentric rings of wildflower displays unmistakably reveal the presence of vernal pool terrain (Holland & Jain 1988). Holland (1978a; 1978b) states that vernal pools were apparently a common feature in most of the Central Valley in presettlement times, estimating that nearly one-third of the valley historically supported them. However, vernal pools in other regions of the state have not been studied as thoroughly, so we cannot adequately assess their historic range and estimate habitat loss.

In southern California, Ferren & Fiedler (1993) estimate that as much as 90% of the vernal pools have been destroyed in the past century. In San Diego County, vernal pools were once common on coastal terraces and inland valleys (Purer 1939). Many have been destroyed by development. Current estimates indicate over 93% of the county's vernal pool habitat has been extirpated, and many of the remaining pools are highly disturbed (Bauder 1986). The situation is similar in Orange County. Aerial photographs of northwestern San Diego and southwestern Orange counties taken prior to extensive urbanization (1932 Whittier Collection; 1941 USGS; 1953 USDA; 1964 California Coastal Commission) show widespread fields of mima mounds, indicating extensive historical vernal pool habitat.

Vernal pools are well known in San Diego and Riverside counties, but not in Orange County, where the pools have remained undocumented. This overlooked habitat has been omitted in important studies of critical plant communities, such as Horn, *et al.* (1993) and Sawyer & Keeler-Wolf (1995). Evans & Bohn (1987) identified mima mound topography in southern Orange County, and Marsh (1992) described remnant or extirpated pools from the Laguna Beach area and Dana Point. Marsh (1992), however, did not cite any of the vernal pool obligate species discussed by Zedler (1987) and therefore, could not authenticate the presence of true vernal pool habitat. Marsh (1992) believes that vernal pools were once common in southern Orange County.

Remnant Orange County terrace vernal pools were identified during this study utilizing aerial photography provided by G. Kuhn (1993, pers. collection), soil survey, and herbarium specimen data. Several pools were documented between

Rancho Laguna and the City of San Clemente only during the unusually wet 1992-1993 rainfall season (Orange County Environmental Management Agency 1996). Aerial photographs taken prior to urbanization in south-central Orange County (City of Irvine, University of California Campus) depict vernal pools (1971, W. Bretz-NRS Collection). Other vernal pools recently recorded from Orange County occur at Whiting Ranch and O'Neil Park (Jones & Stokes 1993), and in Fairview Park, Costa Mesa, (Bowler, *et al.* 1995). A series of small pools also occur near the Badlands Park in Laguna Beach (P. Bowler, pers. comm.). The remaining vestige of pools in Orange County are possibly remnants of a once broader complex of coastal terrace habitats that has been nearly extirpated because of urbanization and agriculture. Soil surveys show that vernal pools in coastal southern Orange County are developed primarily over the very slowly permeable, moderately alkaline Myford sandy loam or the moderately slowly permeable Botella clay loam (Soil Conservation Service 1978). A map and detailed study of the flora of these pools is in preparation.

THE ORIGIN OF MIMA MOUNDS

Mima mounds are the elevated, often circular areas between vernal pools that are composed of unconsolidated fine soils; the term mima mounds originates from their type locality, Mima Prairie, near Olympia, Washington (Dalquest & Scheffer 1942). Mima mounds and vernal pools are inexorably intertwined; there are no mounds without intervening depressions. In California, the intermound depressions are also known as hogwallows (Arkley & Brown 1954; Brandegee 1890; Cox 1984a). Although climate is key for the formation of vernal pools, topography is also important, since pools mostly form in closed depressions (Zedler 1987). In North America, mima mounds are recorded only west of the Mississippi River ranging from southern Canada to northern México (Cox & Scheffer 1991).

Studies of mima mound formation have produced a number of controversial theories about the origins of the mounds. Washburn (1988) provided a comprehensive review, and Berg (1990) grouped theories into four categories: 1) depositional; 2) erosional; 3) periglacial; and 4) biological. Cox (1984b), Zedler (1987), and Holland & Jain (1988) described mound-building processes pertinent to California including origin by: 1) wind deposition near the base of shrubs; 2) groundwater pressure; 3) the activities of fossorial rodents; 4) fracture patterns in the underlying hardpan; 5) expansion and contraction of clay minerals upon wetting and drying; and 6) subsurface mass movements such as soil-piping. Zedler (1987) proposed that differential weathering and settling is primarily responsible for mounded topography in California and presented a model for mound origin by weathering. Each one of the foregoing theories can be locally confirmed by data from particular localities, but none hold true for all situations (Holland & Jain 1988). In recent years, however, only the fossorial rodent hypothesis has received broad acceptance (Dalquest & Scheffer 1942; Arkley & Brown 1954; Barry 1981; Cox 1990).

According to the fossorial rodent hypothesis (Cox 1984; Cox & Scheffer 1991), moundfields originate in shallow soils where pocket gophers build nest sites to escape predation and weather. The nest sites become the center of fixed territories. Subsequently, gophers mine and translocate soil in slow centripetal fashion toward

nests. This tunneling translocates soil, which in time, builds mounds until the centripetal soil-mining activities are balanced by unknown factors (Cox & Scheffer 1991). Cox (1984a,b) has provided evidence that mound formation by foraging rodents is plausible; estimating a typical mound could be formed in approximately 108 years. Extensive behavioral documentation of gophers by numerous researchers has apparently corroborated the pocket gopher theory (Gregory, *et al.* 1987; Hansen 1962; Howard & Childs 1959). Scheffer (1958) and Cox & Scheffer (1991) believe that mima mound terrain occurs only where rodents are, or have been, working the soil.

Although there is an extensive literature discussing the biogenic origin of mounded landscapes, geologists have remained skeptical. Berg (1989) proposed that mounded landscapes are formed when strong seismic activity occurs in areas where a shallow mantle of loess or other fine unconsolidated material overlies a relatively rigid, planar substratum. The substratum could be hardpan, bedded gravel, or bedrock. Berg (1990) then presented data showing that the circular shape and the uniform pattern of mounds can be explained by Richter's (1958) theory of seismic wave motion. According to Berg (1990), the distribution of mima mounds in the United States is directly correlated with regions of moderate to high seismicity. The seismic hypothesis could account for the presence of mima mound-type topography in a wide variety of global geomorphic and climatic provinces and could also explain mound uniformity and soil profiles of mima mound landscapes that cannot be easily demonstrated by the pocket gopher or other theories.

Recently, Kuhn, *et al.* (1995a) identified liquefaction-related features including fissure fills and lateral spreads in mima mound terrain near Carlsbad, San Diego County, in coastal southern California. Paleo-liquefaction, as postulated by these authors, is conspicuous at the Carlsbad site as widespread and abundant injection dikes composed of fine grained white sand, inferred to be ancient beach sand, thrust through the plastic clay-rich surficial deposits; the injection dikes are "sand blow deposits," previously described by Fuller (1912) and Sieh (1978). Existing sand blow deposits (mima mounds) are correlated with the extent of an ancient intertidal lagoon. Kuhn, *et al.* (1995b) hypothesize that during or since the Holocene, mima mound formation due to liquefaction only occurred rarely, when a strong earthquake coincided with unusually high rainfall and perched water conditions far above modern groundwater levels. Although the age of the liquefaction event(s) remains to be determined precisely, the size of the sand blow deposits, the area affected, and the uplift of ancient intertidal deposits imply that coastal uplift and mima mound formation occurred as a result of large, infrequent pre-historic earthquake(s) of magnitude seven or greater. Legg, *et al.* (1994) and Kuhn, *et al.* (1995a) suggest that the source of seismic activity may well be the Newport-Inglewood/Rose Canyon fault located four to six kilometers off the southern California coast. Later studies by Kuhn, *et al.* (1995b) have identified paleo-liquefaction features which extend upward into a series of regressive continental deposits that overlie flights of marine terrace platforms ranging in elevation from 10 to 60 meters. Cross-cutting stratigraphy and relative weathering show at least three epochs of paleo-liquefaction in this region that have displaced very old Indian middens and other archaeological sites (Kuhn, *et al.* 1995b). Thus, major Quaternary deformation of the southern California coast induced during large strike-slip earthquakes are recorded by liquefaction features which could be important in the formation of vernal pools located on higher terraces in Orange and San Diego counties.

Norwick (1991) described the relationship between vernal pool formation and geomorphic processes. He identified ongoing tectonic activity, including development of surface folds and shutter ridges (when a fault moves rock masses horizontally across a valley) with the formation of sag ponds, vernal pools, and swale topography. Norwick's "sand volcanos" and liquefaction craters described from the San Andreas Fault zone were formed during the earthquake of 1906, and apparently predate other intermittent pools of the region. Sieh (1978) also identified liquefaction-related features, including sand blow deposits, as by-products of slip along the San Andreas fault.

Previously, Fuller (1912) studied the succession of shocks collectively designated as the New Madrid earthquake, which occurred between 1811 and 1812, in the central Mississippi Valley in an area encompassing portions of Missouri, Arkansas, Kentucky, and Tennessee. No other feature of the New Madrid region is so conspicuous or widely encountered as the "sunk lands" which resulted from local settling or warping of alluvial deposits (Fuller 1912). Sunk lands are characterized by major alterations to or creation of wetland habitats in clayey alluvial deposits that were still evident 100 years following the shocks. These include sand sloughs, river swamps, sinks, lakes, and ponds. Fuller also describes in great detail sand blows and fissures, which are presently interpreted as relict features of liquefaction events (Obermier 1989). Fuller cites numerous historical accounts of fields composed of sandy mounds, including (pg. 81): 1) "In several places the [sand] blows so obstruct the drainage as to cause the water to collect in shallow pools throughout the wet season."; 2) "The [sand] blows were so thick as to touch, giving rise to many irregular depressions, in some of which considerable pools of water accumulate."; and (pg. 83) 3) "The country here was formerly perfectly level and covered with prairies of various sizes dispersed through the woods. Now it is covered with slashes (ponds) and sand hills or montecules, which are found principally where the earth was formerly the lowest. . . ." The sand blow regions coincide with Berg's (1990) regions of past moderate to high seismicity. Fuller also documents sand craterlets formed near San Francisco in the earthquake of 1906.

The seismogenic origin of mounded landscapes proposed by Berg (1990) and Kuhn, *et al.* (1995b) works also for coastal southern California. It is plausible that the origin of mima mound terrain is, in part, a product of paleo-liquefaction induced by large pre-historic earthquakes, possibly occurring since the Holocene. The impact of shaking on mound-pool terrain could produce settling of fine mound sediments even when earthquakes are not powerful or when they do not coincide with perched water conditions. If mima mounds in coastal southern California were originally formed by successive episodes of liquefaction (presumably southern California has been subjected to large seismic events which induced mound-pool formation long before the Holocene), what ongoing factors operate to maintain the circular profile and height of mounds and deter siltation of fine sediments and sand into intermittent pools? We suggest a biogenic maintenance of liquefaction-mounded landscapes by the activities of fossorial rodents.

As discussed above, evidence has been accumulating for decades indicating that pocket gopher activity is associated with mima mound terrain (Dalquest & Scheffer 1942; Arkley & Brown 1954; Barry 1981; Cox 1990). Soil mining and translocation within "mima mounds" by pocket gophers could replace fine sediments easily lost to erosion, accounting for the long-term maintenance of the mounds' circular form and

height. Tunneling and soil translocation may also impede the otherwise inevitable siltation of intermound basins. Cox (1984b) believes the activities of fossorial rodents create intermound basins while Kuhn, *et al.* (1995a) state that some vernal pools originate over liquefaction-related laterally spreading clays.

Kuhn (unpublished data) has observed vacant rodent burrows in liquefaction terrain in southern California. Abandoned or declining gopher populations in mima mound terrain could produce a mosaic of swales and cloudy silt-pools that provide favorable habitat for other organisms including fairy shrimp, but not for vernal pool obligate plants. Some species of fairy shrimp are not randomly distributed in natural temporary ponds but may favor pools with turbid water to avoid Notonectid (*i.e.*, backswimmer) predation (Woodward & Kiesecker 1994). Shallow silt-pools lack inundation regimes necessary to sustain year to year vernal pool obligate plants except during abnormally high rainfall years. However, cloudy later succession "seres" of intermittent pools could be important in the distribution of vernal pool plants and other species which lack long-distance dispersal mechanisms by providing local habitat patches in the chain of biological archipelagoes. Seed and other propagules could be dispersed between vernal pool "islands" by birds (Baker, *et al.* 1992). Study of liquefaction terrain could afford insight into abiotic and biotic processes affecting possibly coevolutionary biological interactions in earthquake landscapes.

The widely accepted hypothesis that the origin of mounded topography and associated intermittent pools in California is the result of only a single or simplified process should be reevaluated. Vitek (1978) also concluded that mounded topography may result from various processes, and Fuller (1912) described the differences in the genesis of sand blow mounds and prairie mounds. In California with its complex geologic history, mound-depression landscapes can be attributed to numerous and often complementary processes, so that interacting biotic and abiotic processes need to be quantified at each site. In coastal southern California on high geomorphic surfaces (pre-Holocene), mound topography could have a complex origin; mounds may have formed when the surfaces were at low elevations, particularly in sandy sediments conducive to liquefaction, but after uplift, the mounds would have been modified by fossorial rodent activity (R. Shlemon, pers. comm.). Mima mounds and pools developed on specific geologic formations or soil series with different inundation regimes, water-retention capacities, stability and sediment shedding characteristics would be expected to support distinctive floras and faunas.

Liquefaction-origin pools developed in sandy substrates are prone to wetted-clay slip and external drainage; human disturbance could easily reduce the frequency and duration of ponding in vernal pools. As a result, liquefaction-terrain vernal pools may not be recognized readily and their accompanying biota could be overlooked; clearly, this has been the case in Orange County. Mima mounds composed of white or tan fine sands occurring in proximity to major fault zones or in soils without an argillic horizon, especially those on coastal terraces or inland dunes, may be suspected of liquefaction origin (G. Kuhn, pers. comm.). Aerial photographs depicting white, circular spots may indicate remnant mima mounds (*i.e.*, sand blow features) that have been mechanically bladed or disced (Kuhn, *et al.* 1995a). Vernal pools on uplifted marine terraces in the San Diego area previously discussed by Purer (1939) should also be inspected for liquefaction features.

FLORISTICS AND ECOLOGY OF CRYPTOGAMIC VEGETATION IN VERNAL POOL TERRAIN

One of the most widely discussed topics of California natural history is the distinct, concentric assortment of vascular plant species which describe subtle topographic gradients in vernal pools. In southern California the floras of vernal pools differ (Bauder 1987), but whatever species are present selectively inhabit micro-niches or broad radial zones related to inundation regimes, and perhaps, nutrient availability. Kopecko & Lathrop (1975) describe five habitat zones for vascular plants in vernal pools on the Santa Rosa Plateau in western Riverside County, but cryptogamic species also display this kind of zonation.

Cryptogams in vernal pools have scarcely been studied in California, and their contribution to the ecology of this ecosystem has been severely neglected and warrants immediate attention. A preliminary survey of southern California vernal pools suggests a cryptogamic community dominated by cyanobacteria, bryophytes, and cyanophilous lichens (lichens that have blue-green algae photobionts) occupy zones similar to those of the specialized vascular plants. Kopecko & Lathrop's (1975) "muddy margin zone" and the "vernally moist zone" are occupied and often temporarily dominated (extending from the pool basin to mesic margin) by such organisms including species of *Nostoc* (cyanobacterium), *Scleropodium* (moss), *Microcoleus* (cyanobacterium), *Fossombria* (liverwort), *Collema* (cyanolichen), *Riccia* (liverwort), *Funaria*, *Bryum*, and *Ceratodon* (mosses). *Nostoc*, *Leptodictyum* (moss), *Microcoleus*, (?) *Fissidens* (moss), and *Scleropodium* often thrive in the "vernally standing water zone" of vernal pools, and species of *Bryum*, *Funaria*, and *Microcoleus* are common invaders of the "drying marsh bed." A narrow, ephemeral band of bryophytes dominated by liverworts which occurs between the "muddy margin and vernally moist zones" indicates seasonal or year to year fluctuations in precipitation. Lichens most frequently become a prominent feature in the "dry grassland/scrub zone" of undisturbed vernal pool landscapes and may include species of *Acarospora*, *Catapyrenium*, *Collema*, *Cladonia*, *Psora*, *Toninia*, and *Trapeliopsis*. The lichens are successional dominant to mosses and even certain grass and forb species in specialized habitats (Coker 1966; During & Van Tooren 1990; Watt 1937), such as southern California coastal cliffs, dunes, volcanic tablelands, and littoral communities, but are not dominant in inundated areas of vernal pool landscapes. Later successional bryophyte species and cyanophytes such as *Microcoleus vaginatus* (Vauch.) Gom. are also important in native grasslands and scrub in southern California. The absence of cryptogamic flora from suitable habitats in and around vernal pools indicates disturbance and/or alteration of hydrologic cycles by human activities including habitat fragmentation, grazing and discing, alteration of the fire ecology, and air pollution (Bowler & Riefner 1990). It should be noted that pristine floras such as the Morro Bay region in San Luis Obispo County support nearly 375 lichen taxa (Riefner, in prep.); the depauperate list of cryptogams presented in this paper is typical of urban environs in coastal southern California.

Cryptogamic soil crusts (also called biological, cryptobiotic, organogenic, and microphytic crusts) are formed by complex communities of several groups of microphytes including mosses, lichens, liverworts, fungi (including mycorrhizal fungi), green algae, cyanobacteria (blue-green algae), and bacteria. Soil crusts are

common in arid and semi-arid landscapes, and when well-developed, cover the ground with an almost continuous sheet of photosynthetic machinery equivalent to a layer of phanerogamous leaves (Lange, *et al.* 1994). Although usually not thicker than a few millimeters, soil crusts play a decisive role in the functional ecology of arid ecosystems, including cycling of nutrients (especially nitrogen), soil aggregation and stabilization, carbon gain in large areas (Eldridge & Greene 1994; Lange, *et al.* 1992; Beymer & Klopatek 1991), and soil fertility and microbial food webs (Harper & Marble 1988; Johansen 1993; Belnap & Gardner 1993; Belnap 1995). More importantly, cryptogamic crusts deter surface evaporation by sealing the soil surface, and improve overall moisture storage (Lange, *et al.* 1992). During rains, these crusts produce a high yield of runoff percolation which does not occur if crusts are broken or absent (Yair 1990; Lange, *et al.* 1992). Claims of reduced erosion and improved water relations due to cryptogamic vegetation have been widely reported in the literature, but until recently, the evidence has been largely circumstantial. Several authors, however, have recently described and experimentally reproduced the mechanisms by which cryptogams protect the soil and regulate water flow (Chartes & Mucher 1989; Eldridge & Greene 1994; Tchoupopnou 1989; Kinnell, *et al.* 1990; Yair 1990). Thus, the presence or absence of cryptogamic crusts in arid regions can influence the hydrologic cycles of total landscapes including soil erosion (Cameron & Blank 1966; St. Clair & Johansen 1993; West 1990). Despite their importance and widespread distribution, our present knowledge of the species composition and mode of life of cryptogamic crusts is extremely limited in California where research has largely focused on the study of higher plants.

In undisturbed vernal pool landscapes cryptogamic crusts are often a prominent feature that are easily destroyed by grading, discing, grazing, alteration of the fire ecology, and trampling. In a dry climate, human alteration of gently mounded topography characteristic of vernal pool terrain can easily disrupt the delicate balance of specialized hydrophytes inhabiting the narrow radial zones of shallow pools. Additional loss of rain inception and runoff generated percolation historically produced by cryptogamic crusts may dramatically influence the hydrologic status of disturbed vernal pools in southern California, where the average rainfall is markedly less than in the northern part of the state. Increased erosion and decreased aggregate soil stability associated with degradation of cryptogamic communities of disturbed sites (Eldridge & Greene 1994; Kinnell, *et al.* 1990) could also negatively affect the biology of vernal pool terrain. The impact of severe erosion in vernal pool terrain is likely to be greater due to increased transport of organic nitrogen by eroded sediments where the erosional products are nutrient-rich silt and clays rather than sand (Burwell, *et al.* 1975; Pallis, *et al.* 1990; Kinnell, *et al.* 1990). Disturbance of soil surface crusts can also affect vascular plants due to disruption of food webs and alteration of the soil microbiota including mycorrhizal and rhizosheath associations (Allen 1991; Fitter 1977; Grime, *et al.* 1987; Hardie & Leyton 1981; Hartnett, *et al.* 1993), decreased water availability and nutrient uptake in vascular plants (Belnap 1995; Harper & Pendleton 1993; Rogers & Burns 1994), and decreased germination and seedling establishment (Lange, *et al.* 1994; Harper & Pendleton 1993; Rogers & Burns 1994; West 1990). The absence and/or reduction of cryptogamic crusts throughout much of southern California's remaining vernal pool landscapes raises many questions critical to the long-term management of this threatened, arid-land resource.

The microphyte-rich communities inhabiting southern California's vernal pool landscapes support several interesting, strongly interacting associations occupying the

muddy margin and vernal moist zones which could potentially affect the biology of other pool species. During an ongoing investigation of vernal pools in southern California, observations by the senior author of several undisturbed and disturbed pool complexes indicate the dominant constituent of these crusts, the cyanobacterium (blue-green alga) *Microcoleus vaginatus*, could influence or directly regulate several microscale gradients which affect seed plants competing for limited resources in narrow zonal boundaries. This paper presents several mechanisms by which cryptogamic crusts dominated by *M. vaginatus* regulate microscale gradients including water relations, nutrient availability, microbial processes and soil microbiota, soil temperature, safe-site seed selection, and seedling enhancement in vernal pools.

Microcoleus vaginatus is a filamentous, black, mat-forming species which secretes a mucilaginous polysaccharide material from a network of filaments which bind other microphytes and fine sediments into a well-developed crust (Belnap 1993a). *Microcoleus vaginatus* commonly comprises the major component of cryptobiotic crusts in many western states (Belnap 1993a). The success of this cyanophyte in occupying a wide habitat range is due to its resistance to temperature extremes, hypersalinity and alkalinity, desiccation, and to modest nutrient requirements (Carr & Whitton 1982). *Microcoleus* is ubiquitous, and the crust is often inconspicuous as a dark film in the "dry grassland zone" of Kopecko & Lathrop (1975). *Microcoleus*, however, develops a conspicuous mat or crust in vernal moist to inundated clay depressions in grasslands, alkaline sinks, and vernal pools if alternating cycles of wetting and exposure are present which favor rapid filament and sheath production. During the aquatic phase of vernal pools, *M. vaginatus* is often the locally dominant organism forming extensive mats over a broad zone extending from the outer pool edge to standing pool water. As ponded waters fluctuate, the *Microcoleus* colony simultaneously swells into a motile mat covering exposed mud to reach favored photic zones. During the drying phase of vernal pools as the perimeter retreats, *Microcoleus* does also, often coinciding with the germination of vascular plants. The desiccating mat forms a crust/shell over saturated pool soil, deterring evaporation and enhancing the life of an anaerobic zone which inhibits upland vascular plants from colonizing pool margins, and importantly, promotes growth of vernal pool obligates by providing fuel in the form of ammonia. After completely drying, "the dry marsh bed" of shallow pools is often richly covered by *Microcoleus*, and in late spring and summer the curling crusts are a conspicuous feature of many alkaline sinks and vernal pools. This feature could be useful for identifying seasonal wetlands and perched water conditions in southern and central California.

Two key ecophysiological characteristics of *Microcoleus vaginatus* could account for possible mechanisms that effect important microscale gradients.

(1) *Microcoleus vaginatus* produces a large, distinct, sticky extracellular sheath that surrounds groups of living filaments (Belnap 1992). Sheath material rapidly absorbs water, and when wetted, swells, then mechanically extrudes through or over the soil; as the substrate dries the filaments secrete additional mucilaginous material. Rewetting repeats this cycle. *Microcoleus vaginatus* frequently develops a mat or drying crust several millimeters thick due to the recurrent flux of vernal pool waters. *Microcoleus* is capable of growing up to five centimeters in 24 hours (Belnap, *et al.* 1993b) when wetted which enables it to reach favorable photic zones along fluctuating or subsiding pool waters. These adaptative mechanisms may maintain the mat in an

active state in exposed circumstances during alternating cycles of inundation and exposure.

(2) A second trait of *Microcoleus vaginatus* and other cyanophytes is the ability to fix atmospheric nitrogen throughout most of the year (Fuller, *et al.* 1960). Cyanophytes produce nitrogenase, an enzyme complex responsible for catalyzing the conversion of dinitrogen to ammonia. Nitrogen fixation is a stringent anaerobic process, and since *M. vaginatus* lacks heterocysts (thick-walled cells that exclude oxygen), an anaerobic microenvironment must be supplemented in other ways for nitrogenase activity to produce ammonia. Belnap, *et al.* (1993b) has postulated that *M. vaginatus* creates an oxygen-free zone by packing multiple filaments within thick extracellular sheaths or packing groups of sheaths together which has been demonstrated by the morphologically similar oceanic species *Microcoleus chthonoplastes* (Paerl 1985, 1990; Paerl, *et al.* 1991; Pearson, *et al.* 1981). Nitrogenase and N-fixation activity may be closely related to growth of new sheath material and/or new filaments produced only when this cyanophyte is wetted (Belnap, unpublished data). Asexual reproduction by mat expansion acts as a nitrogen source and sink which is mobilized by the presence of water.

Several other nitrogen-fixing lichen and cyanobacteria species are present in vernal pool habitats including *Nostoc* sp. (which does develop heterocysts not requiring constant anaerobic conditions) and the cyanolichen *Collema tenax* (which hosts *Nostoc* as its phycobiont). The cyanolichens apparently occur in numbers too small to contribute significant fixed nitrogen into this system, but species of *Nostoc* may, particularly in deeper static pools. *Nostoc*, previously discussed by Zedler (1987), is a colonial cyanophyte visible in vernal pools or more frequently along the edge of drying pools as small translucent balls. *Nostoc* is well documented for salinity tolerance, importance in nitrogen fixation, and use as a biofertilizer (Singh 1961; Singh, *et al.* 1996).

Microcoleus may serve an important function in the population structure of many vascular plants competing in zonal boundaries and microhabitats of vernal pools. The rapid growth and mat/crust-formation of *M. vaginatus* not only deters evaporation but maintains and enhances an anaerobic environment for itself and associated seed plants in microzones. These affects, in concert with specialized germination requirements, perpetuate native annuals and exclude exotics, and explain the resistance of vernal pools to upland plant invasion. Most importantly, ammonia enrichment produced by *Microcoleus* could alter competitive interactions and provide fuel for the explosive growth and reproduction of vernal pool annuals. Numerous studies have demonstrated that the nitrogen fixed by cyanobacteria is available to and is used by neighboring vascular plants (Fuller, *et al.* 1960; Maryland, *et al.* 1966; Maryland & McIntosh 1966; Stewart 1967). Also, nutrient uptake of seed plants associated with cyanobacterial crusts has been demonstrated to show higher concentrations of many essential macronutrients (Harper & Pendleton 1993; Belnap 1995). In some ecosystems, these crusts have been demonstrated to be the dominant source of limiting elements for seed plant communities (Evans & Ehrlinger 1993). In other studies, Lange (1974) demonstrated that compounds in the gelatinous cyanobacterial sheath material were able to chelate elements essential for growth. Since both clay particles and organic material are negatively charged, the sheath material electrostatically absorbs positively charged essential nutrient ions and holds them in a form available to higher plants (Lange 1976). The sheath material of *Microcoleus* may also enhance the

availability of iron to vascular plants (Belnap & Harper 1994). Chelation of iron may be especially important in alkaline soils (such as the vernal pool soils within the study region) since iron is usually bound in forms unavailable to seed plants (Wallace 1956). Belnap (1992) also showed that mucilaginous sheath material is often coated with negatively charged clay particles, providing a mechanism for retaining positively charged macronutrients in the upper soil profiles that are otherwise prone to leaching.

'Swelling *Microcoleus* mats following the retreating pool-edge waters during the "drying phase" slow evaporation, extend the wet-life of a pool, and may also produce radially-zoned rings of nutrients, inducing certain assemblages of seed plants adapted to specific requirements. A reduction in fecundity in *Limnanthes* and *Orcuttia* due to moisture stress (Brown 1976; Griggs 1976) may be moderated by *Microcoleus* crusts. Linhart (1972; 1974) provided evidence that genetic differences within populations of *Veronica peregrina* L. are adapted to specific environmental conditions differing between pool edge and basin, and may be attributed to nutrient and competition gradients. Linhart (1976) also documented that *Lasthenia* and *Downingia* have greater numbers of viable seed per head at the periphery than at the center of vernal pools. The mucilaginous mat filaments may also act as a seed trap incorporating minute seeds between the polysaccharide sheath material. Lin (1970) noted that certain *Limnanthes* species are restricted to well-defined, smaller vernal pools with conspicuous radial zonation. Seed size, micromorphology, and ornamentation in semi-aquatic plants illustrate the role of safe-site selection (possibly zonation and micro-site establishment) and colonizing ability dependent upon nutrient enriched zonal areas. Thus seed trapping in crusts, and the resulting nitrogen sink, represents an important sequestering of resources which could otherwise be lost in upland areas.

The black mats/crusts of *Microcoleus vaginatus* may also stimulate vascular plant growth and nutrient uptake by producing warmer soil temperatures during the growing season especially at higher elevations or in cooler coastal fog zones. Dark-crusts surfaces have been demonstrated to be significantly warmer than light-colored, non-crusts ones (Belnap 1995). Surface temperatures may be very important, since nitrogenase activity is an extremely temperature dependent process (Rychert, *et al.* 1978). Altered soil temperatures can also effect microbial activity and affect plant germination rates and seedling growth, since timing in vernal pool plants is essential for establishment; relatively small delays in germination can reduce species fitness and seedling establishment (Bush & Van Auken 1991). Because pool temperatures tend to follow changes in air temperature differences more closely than other aquatic environments, *Microcoleus* mats could moderate mud surface temperature fluctuations between pool center and periphery during dry-down (Alexander 1976, Linhart 1976).

Consequently, disturbance of *Microcoleus* mats/crusts can affect moisture status, nutrient availability, seed trapping and germination, seedling establishment, and competitive community structure allied to microzones developed during the recurrent flux of perimeter pool waters. This, in turn, could profoundly affect small annual seed plants in highly competitive vernal pool zones. Since vernal pool annuals produce seeds that germinate in standing water or saturated soils, and most exotic taxa do not, moisture maintenance by specialized crusts is an important resource in excluding exotic plant invasion at the pool ecotone between inundated and non-inundated habitats. Alteration of pool hydrology via reduced precipitation infiltration due to loss of cryptogamic crusts inhabiting open ground characteristic of native grasslands, may also negatively affect subsurface flows and dry-down timing in vernal pools by

decreasing water storage capacities in certain landscape types, especially in shallow soils. Subsurface flows generated by the surrounding watershed which recharge pools by lateral movement of water are important in southern California (Hanes, *et al.* 1990; Zedler 1987). Decreased infiltration rates and subsurface flows could negatively alter pool hydrology following the initial pool filling by rainfall. Pools located in native grasslands, *i.e.*, the Santa Rosa Plateau, which support diverse cryptogamic vegetation characteristic of the habitat (Riefner, unpublished data), may have increased water infiltration compared with bare or disced ground. This could significantly influence the recurrent flux of pool waters over the course of the season and contribute to pool diversity/productivity in the more arid southern portions of the state. Soil water retention capacity in combination with other biotic, geologic, edaphic, and climatic factors may significantly influence the amount and timing of subsurface flows which are important in supplementing direct precipitation and offsetting evaporative loss from pools (Hanes, *et al.* 1990).

According to terminology presented by Westman (1987), *Microcoleus vaginatus* would be identified as a "keystone species" (*i.e.*, the addition or the removal of this species could result in marked changes in community structure and function). Paine (1980) proposed that "modules" may exist within a community. Species dependent upon a common suite of resources, which disappear with the removal of a strongly interacting species, or appear with its addition, belong to a module (Paine 1980). Although there have been few detailed studies describing cryptogams as keystone species for vascular plants, a classic example is the moss *Sphagnum*, which controls the vegetation of bogs at every stage of development by impeding drainage and creating an acid habitat (Crum 1976). Recent research, however, has identified the reindeer lichen, *Cladonia rangiformis* Hoffm., as an important regulator and a keystone organism of lowland heath communities in the United Kingdom (Newsham, *et al.* 1995). Quantitative and empirical evidence discussed by Riefner & Bowler (1995) and Knops, *et al.* (1991) indicate that the fruticose (bush-like or pendulous) lichens *Niebla cerucoides* Rundel & Bowler and *Ramalina menziesii* Taylor improve moisture status and nutrient availability for vascular plant species occupying coastal cliffs and oak savannas (respectively) which concur with Westman's (1983) speculations that relatively minor differences in moisture availability between habitat sites may be sufficient to select for specific species. Vascular plant species inhabiting vernal pool zones affected by *Microcoleus* possibly include *Limnanthes* and *Plagiobothrys* in outer pool margins, and *Myosurus* and *Psilocarphus brevissimus* Nutt. which often germinate in drying cyanobacterial crusts following retreating waters. *Microcoleus* mats/crusts and associated seed plants occupying a broad radial-zone between the edge of the vernal moist zone and the muddy margin of retreating pool waters could be considered a module. The *Microcoleus* module may affect disturbed pools or clay borrow pits in the way the native nitrogen-fixing lupine (*Lupinus arboreus* Sims) alters succession by nutrient enrichment of its habitat (Maron & Connors 1996).

DISCUSSION

We propose that much of the mima mound-type topography in coastal southern California is a geologically young, dynamic landscape which formed as a result of

paleo-earthquake and liquefaction events. Conservation and management of pocket gopher colonies may play a key role in perpetuating vernal pool basins and mimosa mound terrain in this region. The crater pools described by Norwick (1991), as well as other pools known to have filled rapidly with silt, should be examined for evidence of pocket gopher activity to support the validity and role of the biogenic maintenance hypothesis. Vernal pool obligate plant species may gradually succumb to altered hydrologic regimes due to increased siltation in uncolonized mound-depression landscapes or in terrain abandoned by gophers. Other successional stages of liquefaction-origin pools, however, provide habitat for plant communities associated with later stages of pool formation and siltation and other organisms such as fairy shrimp. Cloudy, successional silt-pools also deter growth of certain cyanobacteria, including *Microcoleus*, which require clear water (J. Belnap, pers. comm.); thereby resulting in decreased nitrogen and water storage capacities which promote further changes in the floristic composition. Intermediate stages of siltation may be evident when vernal pool obligates appear only during abnormally high rainfall years which temporarily restore the inundation regime necessary for germination. Orcutt (1887) described a similar phenomenon in San Diego which occurred only in the unusually wet spring of 1884 when previously dry hollows and flats produced a luxuriant array of vernal pool species which "withered away to let others succeed when another favorable season should chance to roll around in future years." Earthquake successional sequences and seismogenic tracker species, that may include pocket gophers and fairy shrimp, potentially illustrate complex issues of population coevolution which remains a relatively unexplored topic in vernal pool science. The occurrence of certain locally abundant bulb-forming plants, including species of *Brodiaea* and *Muilla*, near vernal pools is often attributed to substrate preference, but may be in part due to gophers eating and storing plant parts. Previously, Brandegee (1890) discussed the "rooting of hogs" as a possible means of dispersal of *Dodecatheon* species locally distributed about vernal pools in Sacramento County.

Although the productivity of cyanobacterial mats has been described for other habitats experiencing alternate wetting-drying, *i.e.*, tidal flats (Zedler 1980), the role and potential importance of these mats in vernal pools has not been previously described. Microzone formation by *Microcoleus vaginatus* which ensures an anaerobic environment for itself and the ability to fix atmospheric nitrogen brings about a dynamic interplay between moisture storage, nitrogenase and ammonia production, and soil temperature patterns which promote rapid growth and reproduction of annual seed plants in vernal pools. Previously, Jokerst (1993) also speculated that microclimate changes due to alteration of plant cover, soil, water movement, and temperature patterns could conceivably affect herbaceous plant communities of vernal pools. Destruction of cyanobacterial associations may also permanently change composition and productivity in certain pool zones and negatively affect the loss of pool-edge moisture status and associated species. Pools altered by hydrologic and other related factors, *i.e.*, nutrient status, are often invaded by exotic taxa and dominated by relatively large populations of only a few native species. Analysis of vernal pools might assume that habitat quality is positively correlated with species density; this could be misleading for rare species conservation since density alone may not be positively correlated with habitat quality (Van Horne 1983).

Conservation issues involving successional seres of vernal pools are also relatively unexplored. Zedler (1987) considered it a mistake to assume that pools and non-pools are the only category of vegetation in vernal pool landscapes. If late successional or

disturbed silt-pools do support a dormant seed stock of obligate vernal pool species which only rarely germinate except under optimal hydrologic conditions, then these habitats should also be identified and protected, perhaps as a subclass of vernal pools. During drought years in southern coastal California, *Plantago elongata* Pursh may be an indicator of silted, drying liquefaction pools. Twisselmann (1967) indicated that vernal pools in Kern County typically exist for years without water and/or the appearance of vernal pool vegetation. Apparently, there is a continuum of water duration characteristics from which vernal pools in the strict sense and other ephemeral wetlands within vernal pool terrain develop (Zedler 1987). Other organisms, including fairy shrimp, also occupy the full range of intermittent pool types in vernal pool landscapes (Brown, *et al.* 1993). From a conservation perspective, the most practical approach is ecosystem identification proposed by Sawyer & Keeler-Wolf (1995) rather than the simplified vascular plant community classification. Species found in vernal pools that are more abundant outside pool habitat in surface water slope wetlands in coastal sage scrub, i.e., *Eryngium* aff. *vaseyi* J. Coulter & Rose and *Trifolium variegatum* Nutt., may indicate the importance of conserving small ephemeral wetlands or seepage habitats in liquefaction-type terrain. A mosaic of pool complexes incorporating distinct edaphic types and serial stages is suggested.

Cyanobacteria may play an important role in promoting maximum biodiversity in southern California's vernal pools. *Microcoleus* and/or pools designed to duplicate the recurrent flux hypothesis should be incorporated into habitat mitigation plans since artificially created pools frequently lack species abundance and cover comparable to natural pools of the same region (Ferren & Gevirtz 1990; Zedler, *et al.* 1993).

THE FLORA

This preliminary compendium of cryptogamic and phanerogamic flora is the result of surveys conducted between the spring of 1993 and the spring of 1996 at San Clemente and San Onofre State Beaches, and infrequent visits to other Orange County sites listed below. Most noteworthy is the varied composition associated with duripan or claypan soils, and cycles of abundance which vary from year to year. Several of the species recorded during this study appeared only during the unusually wet spring of 1993 (11-inches above-average precipitation; Orange County Environmental Management Agency 1996), possibly due to replenished inundation and germination regimes; other species absent or rare during wet years were recorded only during subsequent drier periods. Rare or regionally uncommon vascular plants of Orange or San Diego counties collected during this study include: *Alopecurus saccatus* Vasey, *Atriplex pacifica* Nelson, *Brodiaea jolonensis* Eastw., *Crassula aquatica* (L.) Schönl., *Deschampsia danthonioides* (Trin.) Benth., *Dudleya blochmaniae* (Eastw.) Moran, *Eryngium* aff. *vaseyi*, *Harpogonella palmeri* A. Gray *Hordeum intercedens* Nevski, *Microseris douglasii* (DC.) Schultz-Bip. subsp. *platycarpa* (A. Gray) Chambers, *Marsilea vestita* Hook. & Grev., *Muilla maritima* (Torrey) S. Watson, *Myosurus minimus* L., *Navarretia prostrata* A. Gray, *Pilularia americana* A. Braun, *Psilocarphus brevissimus*, *Psilocarphus tenellus* Nutt., and *Senecio aphanactis* E. Greene.

Voucher specimens have been deposited in the University of California, Irvine, Museum of Systematic Biology (IRVC) and selected duplicates have been placed in the herbarium of the Rancho Santa Ana Botanic Garden (RSA).

LEGEND

- * Indicates a specialist which is generally restricted to vernal pools or an introduced taxon (!*) characteristic of the vernal pool community in coastal California according to Zedler (1987).
- + Indicates an aquatic generalist that is more common in other aquatic, marsh, or seepage habitats.
- ! Indicates a non-native species that may tolerate inundation/saturation.
- o Indicates a native species occurring in diverse habitats that can tolerate limited periods of saturation/inundation.
- ^ Indicates a native or exotic species that may grow near vernal pools but does not grow in the saturation zone and cannot tolerate extended inundation.
- † Indicates extreme fluctuations in the population size/vigor or the presence/absence of a species recorded during the study period which may be attributed to variation in environmental conditions.

R Rare at the site.

I Occasional to infrequent.

C Common.

SB Surf Beach Unit, San Onofre State Beach, San Diego Duripan Vernal Pools; **Location:** San Diego County. San Onofre State Beach. Surf Beach Unit (San Onofre USGS 7.5' Quadrangle, T9S, R7W, Section 24); **Soils:** Soils are classified as Carlsbad gravelly loamy sand, which is gently sloping and characterized by an iron-silica cemented duripan (Soil Conservation Service 1973).

T Trestles Unit, San Onofre State Beach, San Diego Claypan Vernal Pools and Swales; **Location:** San Diego County. San Onofre State Beach. Trestles Natural Preserve Unit (San Clemente USGS 7.5' Quadrangle T9S, R7W, Section 14); **Soils:** Visalia Series are mapped for this region; these have moderately rapid permeability and support soil inclusions such as Placentia soils which contain a sandy clay subsoil of very slow permeability (Soil Conservation Service 1973).

SC San Clemente State Beach, Orange County Liquefaction-Origin Vernal Pools; **Location:** Orange County. San Clemente State Beach (San Clemente USGS 7.5' Quadrangle T9S, R7W, Section 10); **Soils:** Soils are classified as Myford Series, very slowly permeable, moderately alkaline, with a clay-rich subsoil (Soil Conservation Service 1978).

O Additional Orange County Pools-**Locations:** Rancho Laguna-Laguna Beach (Laguna Beach USGS 7.5' Quadrangle T8S, R8W, Section 31), Dana Hills (Dana Point USGS 7.5' Quadrangle T8S, R8W, Section 10/15), and San Clemente (San Clemente USGS 7.5' Quadrangle T8S, R7W, Section 32); **Soils:** Myford sandy loam, rarely the moderately slowly permeable Botella clay loam (Soil Conservation Service 1978).

PRELIMINARY INVENTORY OF SPECIES INHABITING VERNAL POOLS AND ADJACENT UPLAND TERRAIN

CRYPTOGAMIC PLANTS

CYANOBACTERIA:

	<u>SB</u>	<u>T</u>	<u>SC</u>	<u>O</u>
o <i>Microcoleus vaginatus</i> (Vauch.) Gom., filamentous cyanobacterium	C	C	I	I
+ <i>Nostoc</i> sp., heterocystous cyanobacterium	I	I	R	I

BRYOPHYTES:

o <i>Asterella</i> sp., liverwort	-	R†	-	R
^ <i>Bryum argenteum</i> Hedw., moss	R	C	I	I
o <i>B. bicolor</i> Hedw., moss	-	R	R	R
o <i>B. gemmiparum</i> De Not., moss	-	-	-	I
o <i>B. pseudotriquetrum</i> (Hedw.) Gaertn., Meyer & Schreb., moss	-	R	-	I
^ <i>Ceratodon</i> sp., moss	-	R	-	-
o <i>Ceratodon purpureus</i> (Hedw.) Brid., moss	-	-	R	I
^ <i>Claopodium wippleanum</i> (Sull.) Ren. & Card., moss	-	-	I	I
o <i>Fossombrina longiseta</i> Aust., liverwort	-	I	-	-
o <i>Funaria hygrometrica</i> Hedw., cord moss	R	C	R	I
o <i>Riccia glauca</i> L., liverwort	-	I†	-	R
o <i>R. nigrella</i> DC., liverwort	-	R	R	R
^ <i>R. trichocarpa</i> M.A. Howe, liverwort	-	R	-	I
+ <i>Scleropodium tourettei</i> (Brid.) L. Koch, moss	-	R†	-	-
^ <i>Timmiella crassinervis</i> (Hampe) L. Koch, moss	-	-	-	I
^ <i>Tortula ruralis</i> (Hedw.) Gaertn., Meyer & Schreb., moss	-	-	R	R
^ <i>Weisia controversa</i> Hedw., moss	-	-	-	R

LICHENS: (Terricolous species only; those not marked cyanolichen have green photobionts.)

^ <i>Acarospora</i> cf. <i>schleicheri</i> (Ach.) A. Massal.	-	-	-	R
o <i>Caloplaca</i> sp.	-	-	I	-
^ <i>Catapyrenium lachneum</i> (Ach.) R. Sant.	R	-	-	R
^ <i>Cladonia</i> sp. (sterile), pyxie cups	-	-	-	R
^ <i>Cladonia furcata</i> (Hudson) Schrader	-	R	-	-
^ <i>Cladonia scabriuscula</i> (Delise) Nyl.	-	-	R	-
o <i>Collema</i> sp., cyanolichen	-	R	-	R
o <i>Collema texanum</i> Tuck., cyanolichen	R	-	R	R
^ <i>Diploschistes actinostomus</i> (Ach.) Zahlbr.	-	-	-	I
^ <i>Lecanora</i> cf. <i>argopholis</i> (Ach.) Ach.	-	-	-	R
^ <i>Leprocaulon microscopicum</i> (Vill.) Gams ex D. Hawksw.	-	-	I	R
^ <i>Leproloma</i> sp.	-	-	-	I

^ <i>Psora decipens</i> (Hedw.) Hoffm.	-	R	-	R
^ <i>Rinodina bolanderi</i> H. Magn.	-	-	-	R
^ <i>Trapeliopsis</i> sp.	-	-	-	R

PHANEROGAMIC PLANTS

FERNS:

Marsileaceae, marsilea family

* <i>Marsilea vestita</i> Hook. & Grev. subsp. vestita, clover fern (RSA)	-	-	-	R
* <i>Pilularia americana</i> A. Braun, pillwort (RSA)	C†	-	-	-

MONOCOTS:

Cyperaceae, sedge family

+ <i>Eleocharis macrostachya</i> Britton, pale spike-rush	-	-	R	I
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Iridaceae, iris family

o <i>Sisyrinchium bellum</i> S. Watson, blue-eyed grass I	-	-	C	C
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Juncaceae, rush family

+ <i>Juncus bufonius</i> L. var. <i>bufonius</i> , toad rush (RSA)	C	I†	C†	I
o <i>J. mexicanus</i> Willd., Mexican rush	-	-	-	I

Liliaceae, lily family

^ <i>Bloomeria crocea</i> (Torrey) Cov., common golden star	-	R	C	R
o <i>Brodiaea jolonensis</i> Eastw., mesa brodiaea (RSA)	-	-	I†	R
^ <i>Calochortus splendens</i> Benth., splendid mariposa lily	-	-	C	I
^ <i>Chlorogalum parviflorum</i> S. Watson, soap plant	-	-	I	I
^ <i>Dichelostemma capitatum</i> Alph. Wood, blue dicks	R	-	C	C
o <i>Muilla maritima</i> (Torrey) S. Watson, common muilla (RSA)	-	-	I	I

Poaceae, grass family

* <i>Alopecurus saccatus</i> Vasey, foxtail grass (RSA)	-	R†	-	-
!+ <i>Agrostis viridis</i> Gouan, bent grass	-	-	I	I
^ <i>Avena barbata</i> Link, slender wild oat	C	I	C	C
! <i>Avena fatua</i> L., wild oat	I	I	I	I
!+ <i>Briza minor</i> L., little quaking grass	R†	-	-	-
^ <i>Bromus diandrus</i> Roth, ripgut grass	I	R	I	I
! <i>Bromus hordeaceus</i> L., soft chess	C	C	C	I
^ <i>Bromus madritensis</i> L. subsp. <i>rubens</i> (L.) Husnot, foxtail chess	C	I	C	C
!+ <i>Crypsis schoenoides</i> (L.) Lam., swamp grass	-	-	-	R
!+ <i>Cynodon dactylon</i> (L.) Pers., bermuda grass	R	-	R	-
* <i>Deschampsia danthonioides</i> (Trin.) Benth., annual hairgrass (RSA)	-	R†	-	-
o <i>Distichlis spicata</i> (L.) E. Greene, salt grass	R	-	C	I
! <i>Gastridium ventricosum</i> (Gouan) Schinz & Thell., nit grass (RSA)	-	-	I	R

!+ <i>Hainardia cylindrica</i> (Will.) Greuter (RSA)	I†	-	R†	-
o <i>Hordeum intercedens</i> Nevski, barley (RSA)	C	-	R	C
^ <i>Hordeum murinum</i> L. subsp. <i>leporinum</i> (Link) Arcang., barley	I	-	C	I
^ <i>Lamarckia aurea</i> (L.) Moench, goldentop	R	-	I	I
! <i>Lolium multiflorum</i> Lam, Italian ryegrass	I	R	I	I
!+ <i>Lolium perenne</i> L., perennial ryegrass	C	R	C	I
^ <i>Nassella lepida</i> (A. Hitchc.) Barkworth, foothill needle-grass	-	-	R	R
^ <i>N. pulchra</i> (A. Hitchc.) Barkworth, purple needle-grass	R	-	C	I
! <i>Phalaris minor</i> Retz., littleseed canary grass (RSA)	I	-	-	I
!* <i>Phalaris paradoxa</i> L., paradox canary grass	-	-	-	R
! <i>Poa annua</i> L., annual bluegrass	-	-	I	I
!+ <i>Polypogon monspeliensis</i> (L.) Desf., rabbit-foot grass	C	I	R	R
! <i>Vulpia myuros</i> (L.) C. Gmelin var. <i>myuros</i> , rattail fescue	I	C	I	I
^ <i>V. myuros</i> var. <i>hirsuta</i> (Hackel) Asch. & Graebner, rattail fescue	C	C	C	C

DICOTS:**Amaranthaceae**, amaranth family

! <i>Amaranthus albus</i> L., tumbleweed	-	I	R	R
o <i>A. blitoides</i> S. Watson, prostrate amaranth	-	-	R	R
^ <i>A. deflexus</i> L., low pigweed	-	-	R	R

Anacardiaceae, sumac family

^ <i>Rhus integrifolia</i> (Nutt.) Brewer & S. Watson, lemonadeberry	-	R	I	I
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Aizoaceae, fig-marigold family

^ <i>Malephora crocea</i> (Jacq.) Schwantes, croceum iceplant	I	-	I	-
^ <i>Mesembryanthemum nodiflorum</i> L., slender-leaved iceplant	C	-	I	I

Apiaceae, celery family

* <i>Eryngium</i> aff. <i>vaseyi</i> J. Coulter & Rose, coyote-thistle (RSA)	I	-	-	-
! <i>Foeniculum vulgare</i> Miller, fennel	-	R	R	R

Asteraceae, sunflower family

o <i>Amblyopapus pusillus</i> Hook. & Arn., coast weed	C	-	I	R
o <i>Ambrosia psilostachya</i> DC., western ragweed	-	-	R	R
o <i>Baccharis pilularis</i> DC., coyote brush	R	C	R	R
+ <i>B. salicifolia</i> (Ruiz Lopez & Pavon) Pers., mule fat	-	R	-	-
^ <i>Centaurea melitensis</i> L., yellow star-thistle	I	-	-	R
! <i>Chamomilla suaveolens</i> (Pursh) Rydb., pineapple weed	C	-	R	R
^ <i>Chrysanthemum coronarium</i> L., crown daisy	I	-	-	-
o <i>Conyza canadensis</i> (L.) Cronq., horseweed	R	-	I	R

o <i>Conyza coulteri</i> A. Gray, Coulter's horseweed	-	I	-	-
!+ <i>Cotula coronopifolia</i> L., brass-buttons	C	-	-	R
+ <i>Euthamia occidentalis</i> Nutt., western goldenrod	-	I	-	-
^ <i>Filago californica</i> Nutt., fluffweed	-	I	-	R
^ <i>F. gallica</i> L., narrow-leaved filago	-	C	R	C
! <i>Gnaphalium luteo-album</i> L., weedy cudweed	I	I	R	I
* <i>Gnaphalium palustre</i> Nutt., lowland cudweed	R†	-	-	-
o <i>Grindelia camporum</i> E. Greene var. <i>camporum</i> , gumplant	-	-	C	R
^ <i>Hedypnois cretica</i> (L.) Dum.-Cours., Crete hedypnois	-	-	I	R
o <i>Hemizonia fasciculata</i> (DC.) Torrey & A. Gray, tarweed	C	-	I	I
o <i>Hemizonia paniculata</i> A. Gray, San Diego tarweed	-	C	I	R
! <i>Hypochaeris glabra</i> L., cat's ear	C	C	C	I
o <i>Isocoma menziesii</i> (Hook. & Arn.) G. Nesom var. <i>menziesii</i> , goldenbush	C	-	I	I
+ <i>I. menziesii</i> var. <i>vernoides</i> (Nutt.) G. Nesom, goldenbush (RSA)	-	R	-	R
! <i>Lactuca serriola</i> L., prickly lettuce	I	-	-	R
o <i>Lasthenia californica</i> Lindley, common goldfields	-	-	R	R
o <i>Layia platyglossa</i> (Fischer & C. Meyer) A. Gray, tidy-tips	-	-	-	R
o <i>Micropus californicus</i> Fischer & C. Meyer, slender cottonweed	-	I	R	R
o <i>Microseris douglasii</i> (DC.) Schultz-Bip. subsp. <i>platycarpa</i> (A. Gray) Chambers, small-flowered microseris (RSA)	C	-	R	-
+ <i>Pluchea odorata</i> (L.) Cass., salt marsh fleabane	-	R	-	-
* <i>Psilocarphus brevissimus</i> Nutt. var. <i>brevissimus</i> , woolly-heads (RSA)	C	C	R†	R†
* <i>P. tenellus</i> Nutt. var. <i>tenellus</i> , slender woolly-heads (RSA)	-	I†	R†	R†
o <i>Senecio aphanactis</i> E. Greene, rayless ragwort (RSA)	-	-	R†	R
! <i>Senecio vulgaris</i> L., common groundsel	C	-	C	I
! <i>Sonchus asper</i> (L.) Hill subsp. <i>asper</i> , prickly sow-thistle	I	-	R	R
! <i>Sonchus oleraceus</i> L., common sow-thistle	I	R	I	I
o <i>Stebbinsoseris heterocarpa</i> (Nutt.) Chambers, derived microseris	R	-	R	I
^ <i>Uropappus lindleyi</i> (DC.) Nutt., silver puffs	-	-	R	R
Boraginaceae, borage family				
^ <i>Cryptantha micromeres</i> (A. Gray) E. Greene, minute-flowered cryptantha (RSA)	-	R†	-	-
o <i>Harpagonella palmeri</i> A. Gray, Palmer's grappling hook	-	-	R	R
* <i>Plagiobothrys acanthocarpus</i> (Piper) I.M. Johnston, adobe popcorn flower (RSA)	C	I†	R†	I

^ <i>P. collinus</i> (Philbr.) I.M. Johnston var. <i>fulvescens</i> (I.M. Johnston) Higgins, rough popcorn flower	-	-	R	R
o <i>P. nothofulvus</i> (A. Gray) A. Gray, popcorn flower	-	-	-	R
Brassicaceae , mustard family				
! <i>Brassica nigra</i> (L.) Koch, black mustard	-	-	R	I
o <i>Cardamine californica</i> (Torrey & A. Gray) E. Greene var. <i>integrifolia</i> (Torrey & A. Gray) Rollins, milkmaids	-	-	I	I
o <i>Lepidium nitidum</i> Torrey & A. Gray, shining peppergrass	C	-	I	I
Callitrichaceae , starwort family				
* <i>Callitriche marginata</i> Torrey, wallow starwort	R†	-	-	-
Caryophyllaceae , pink family				
^ <i>Silene gallica</i> L., common catchfly	R	-	I	R
! <i>Spergularia bocconii</i> (Scheele) Merino, sand-spurrey	R	R	I	I
o <i>Spergularia macrotheca</i> (Hornem.) Heynh. var. <i>macrotheca</i> , sticky sand-spurrey (RSA)	-	-	R	R
! <i>Spergularia villosa</i> (Pers.) Cambess., villous sand-spurrey	I	I	C	I
Chenopodiaceae , goosefoot family				
^ <i>Atriplex lindleyi</i> DC., a saltbush (RSA)	R	-	R	-
o <i>A. pacifica</i> Nelson, south coast saltbush (RSA)	-	-	R†	-
! <i>A. rosea</i> L., tumbling oracle	-	-	R	R
! <i>A. semibaccata</i> R. Br., Australian saltbush	C	-	I	I
o <i>A. serenana</i> Nelson, bractscale (RSA)	-	-	R	-
! <i>Chenopodium album</i> L., lamb's quarters	-	-	I	R
! <i>C. ambrosioides</i> L., Mexican tea	-	I	R	-
! <i>Salsola tragus</i> L., tumbleweed	R	R	I	I
Convolvulaceae , morning glory family				
o <i>Cressa truxillensis</i> Kunth, alkali weed (RSA)	-	-	C	I
! <i>Convolvulus arvensis</i> L., bind weed	R	-	R	R
Crassulaceae , stonecrop family				
* <i>Crassula aquatica</i> (L.) Schönl., pygmy stonecrop (RSA)	C†	-	-	-
o <i>C. connata</i> (Ruiz Lopez & Pavon) A. Berger, pygmy-weed	C	I	I	C
^ <i>Dudleya blochmaniae</i> (Eastw.) Moran subsp. <i>blochmaniae</i> , Blochman's dudleya	-	-	I	R
^ <i>D. edulis</i> (Nutt.) Moran, ladies-fingers	-	-	I	I
Elatinaceae , waterwort family				
* <i>Elatine brachysperma</i> A. Gray, waterwort (RSA) I†	-	-	-	R†
Euphorbiaceae , spurge family				
! <i>Chamaesyce maculata</i> (L.) Small, spotted spurge (RSA)	I	I	-	R
Fabaceae , pea family				
o <i>Trifolium depauperatum</i> Desv. var. <i>amplectens</i> (Torrey & A. Gray) L.F. McDermott, pale sack clover (RSA)	C	I	-	R

o <i>T. variegatum</i> Nutt., white-tip clover (RSA)	-	-	R†	-
Geraniaceae , geranium family				
! <i>Erodium botrys</i> (Cav.) Bertol., broadleaf filaree (RSA)	I	-	R	R
^ <i>E. cicutarium</i> (L.) L'Hér., red-stemmed filaree	I	-	I	I
^ <i>E. moschatum</i> (L.) L'Hér., white-stemmed filaree	I	C	R	I
Lamiaceae , mint family				
! <i>Marrubium vulgare</i> L., horehound	-	-	R	I
Lythraceae , loosestrife family				
! * <i>Lythrum hyssopifolia</i> L., loosestrife	C	R	R	R
Malvaceae , mallow family				
! <i>Malva parviflora</i> L., cheeseweed	I	-	I	I
o <i>Malvella leprosa</i> (Ortega) Krapov., alkali-mallow	R	-	R	R
Molluginaceae , carpet-weed family				
!+ <i>Glinus lotoides</i> L., carpet-weed	-	I	-	-
Oxalidaceae , oxalis family				
^ <i>Oxalis pes-caprae</i> L., Bermuda buttercup	R	-	I	R
Plantaginaceae , plantain family				
o <i>Plantago elongata</i> Pursh, alkali plantain (RSA)	C	R	I	I
^ <i>P. erecta</i> E. Morris, California plantain	-	C	-	I
! <i>P. virginica</i> L., plantain (RSA)	-	-	-	R
Polemoniaceae , phlox family				
^ <i>Linanthus dianthiflorus</i> (Benth.) E. Greene, ground-pink	-	-	-	R
o <i>Navarretia atractylodes</i> (Benth.) Hook. & Arn., holly-leaved skunkweed (RSA)	-	-	-	R
* <i>N. prostrata</i> A. Gray, navarretia (RSA)	-	R†	-	-
Polygonaceae , buckwheat family				
! <i>Polygonum arenastrum</i> Boreau, common knotweed	R	R	R	R
!+ <i>Rumex crispus</i> L., curly dock	C	-	R	R
Portulacaceae , purslane family				
o <i>Calandrinia ciliata</i> (Ruiz Lopez & Pavon) DC., red maids	R	-	-	R
Primulaceae , primrose family				
! * <i>Anagallis arvensis</i> L., scarlet pimpernel	C	C	I	C
Ranunculaceae , buttercup family				
* <i>Myosurus minimus</i> L., little mousetail (RSA)	I	-	-	-
o <i>Ranunculus californicus</i> Benth., California buttercup	-	-	R	I
Rubiaceae , madder family				
o <i>Galium aparine</i> L., goose grass	C	-	I	I
Scrophulariaceae , figwort family				
o <i>Castilleja exserta</i> (A.A. Heller) Chuang & Heckard, purple owl's clover	-	-	R	C
^ <i>Linaria canadensis</i> (L.) Dum.-Cours., blue toadflax	-	-	I	I
+ <i>Veronica peregrina</i> L. subsp. <i>xalapensis</i> (Kunth) Pennell, purslane speedwell (RSA)	I†	-	-	-

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